STUDIES ON THE GUT OF

ERIONOTA TORUS EVANS AND *EUPLOEA CORE* CRAMER

(LEPIDOPTERA)

IN RELATION TO METAMORPHOSIS

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ABSTRACT

The gross morphology and histology of the gut in the 5th instar larva, various stages of pupa, and adult of *Erionota torus* and *Euploea core* have been described.

Detailed accounts of the foregut, midgut, and hindgut during metamorphosis have been given. Particular attention have been given to the development of the adult crop and the formation of the proventriculus and oesophageal invagination of the adult. The fate of each region of the larval oesophageal invagination has been traced during the progress of metamorphosis.

Descriptions are made to the replacement of the midgut epithelium during the larval-pupal transformation. The fate of the yellow body is followed.

The development of the larval ileum has been worked out; the cryptonephric condition of the larval rectum and the disassociation of this condition have been examined in detail. The subsequent formation of the adult rectum, particularly the development of the rectal pads, has been investigated.

Functional differentiation of each region of the gut in relation to metamorphosis has also been discussed.

GENERAL INTRODUCTION

Second only to the Coleoptera in number of species, the Lepidoptera is a very large order of insects in the Endopterygota as well as other animals.

It is difficult to tell the exact number of species of Lepidoptera. However, it has been suggested that there exists more than 140,000 species (Smart, 1976) of Lepidoptera. Among these, more than 20,000 species of club-horned butterflies have been recorded. Moreover, Lepidoptera occurs in almost every part of the world. This shows their great adaptations to almost any type of environmental condition as well as their wide range of food habits.

Most of the Lepidoptera larvae are phytophagous. They cause great damages to almost every part of a plant: say, by boring into the stem as Chilo supressalis and Tryporyza incertulas to rice; by gnawing the root as Agrotis ypsilon to vegetables or by devouring leaves as Pieris brassicae to crucifers.

Damages caused by butterflies are of minor importance in comparison with that of moths. However, there are some outstanding cases; such as Pieris conidia

(cabbage white) of crucifers; Parnara guttata (common straight swift) of rice; Lampides boeticus (pea blue) of Leguminosae; Papilio xuthus of citrus; Graphium sarpedon (common blue bottle) of camphor and Ariadne ariadne (angled castor) or castor.

The alimentary canal of an insect is highly adapted to what it eats, thus determining its ecological role (Trager, 1953). A knowledge of the functional morphology and histology of the gut of an insect is therefore remarkably important. As workers such as Hirano (1964) and Cheung (1966) have suggested, a basic knowledge of the nutritional and digestive physiology of insects may be of considerable importance for the development of control measures to check their destruction of things that are essential to man.

Lepidopterous caterpillars are important in the study of economic entomology and have therefore received much attention. The morphology and histology of the alimentary canal of these larvae are well documented (Henson, 1931, 1932; El-Sawaf, 1950; Teotia and Pathak, 1957; Beams and Anderson, 1957; Anderson and Harvey, 1966; Drecktrah et al., 1966; Cheung, 1966; Judy and Gilbert, 1969, 1970; Reinecke et al., 1973; Chi et al., 1975; Ramsay, 1976), but remarkably little is known about the

alimentary canal during metamorphosis. Furthermore, the larve-pupa-adult transformation of Lepidoptera is impressive since the gut changes from a true functional digestive tract in the feeding larva to a more or less vestigial system in the non-feeding pupa and a functional nectar-feeding system in the adult (Judy and Gilbert, 1970).

According to the Chinese legends, the Empress of Huang Ti (The Yellow Emporor, B.C. 2697-2597) was the first observant person who noticed the metamorphosis of silkworm and made use of the silken cocoon thereafter (Kellogg, 1968). In modern science, Malpighi (1669) and Swammerdam (1685) were the first observers of metamorphosis in Lepidoptera. Malpighi studied the internal organs of Bombyx mori while the latter used Pieris brassicae and Vanessa urticae for his observation. However, the morphological changes of the alimentary canal have been less studied while other orders, such as Diptera and Coleptera have received more attention (Deegener, 1904; Perez, 1910; Snodgrass, 1924; Beal, 1927; Mansour, 1927; Bodenstein, 1950; Whitten, 1957b; Romoser and Venard, 1966, 1967; Ameen, 1969; Benham, 1970; Morgan et al., 1970; Ameen and Rahman, 1973; and Becker, 1978).

Butterflies are regarded as more advanced than moths in general (Common, 1975). However, most of the investigations concerning the alimentary canal of Lepdioptera in relation to metamorphosis were those of moths. In this case, it is necessary to study whether the drastic changes of the alimentary canal of butterfly during metamorphosis is similar to that of moth.

Erionota torus Evans of Hesperiidae and Euploea core Cramer of Danainae (Nymphalidae) were chosen for this study. As Common (1975) has pointed out: "In more advanced pupae the degree of movement of the abdominal segments decreases, beginning at the base of the abdomen, until, in the most specilized movement is possible between only two segments or not al all." The pupa of Erionota has freedom of movement between abdominal segments whilst the pupa of Euploea is fixed and no movement was shown even when being disturbed. Moreover, Erionota spins a thin cocoon, which is a characteristic shared with moth in common, before pupation actually takes place. It is obvious that Erionota is more primitive. The changes of its alimentary canal could, therefore, be somewhat different from that of Euploea.

The aims of this investigation are as follows:

1. to study the gross morphology of the alimentary canal during various stages of metamorphosis.
2. to examine the anatomy and histology of the true functional alimentary canal in the feeding larva to that in the nectar-feeding adult.
3. to examine the changes of the ectodermal originated foregut and hindgut during metamorphosis, especially the development of the adult crop and the adult rectum.
4. to examine the development of the endodermal originated midgut.

This thesis is divided into three major parts:

1. Gross morphology of the gut of the two species during metamorphosis:- to show, with illustrations, the gradual changes of the larval gut to adult gut.
2. Histology of the gut of the two species during metamorphosis:- to show histologically the development of each part of the gut.
   a. foregut
   b. midgut
   c. hindgut
3. General conclusion and summary.

PART I

GROSS MORPHOLOGY OF THE GUT

OF *ERIONOTA* AND *EUPLOEA*

DURING METAMORPHOSIS

INTRODUCTION

This chapter is a preliminary study dealing with the gross morphological changes of the gut of Erionota torus and Euploea core during metamorphosis. This study provides a bird's-eye view for the metamorphic changes of the gut and serves as a basis for the histological studies subsequently.

MATERIALS AND METHODS

The eggs and larvae of Erionota torus Evans were collected from local banana cultivation. Larvae hatched out were reared in banana leaves (Musa paradisiaca L. var. sapientum O. Ktze.) rolled up by hand. Each leaf-roll was placed separately in a polythene bag and tied up with rubber band to maintain a satisfactory humidity. Fresh banana leaves were supplied to the young larva every two days while those for fifth instar larvae were supplied every day. The culture was maintained in a wooden rearing chamber in the laboratory with a temperature of $27^{o}C \pm 2^{o}C$ and R.H. 80-85%; and a long day photoperiod of 14 hours was kept. Special attention has been paid to those fully grown fifth instar larvae, which, when stopped feeding, were allowed to pupate.

Adults were collected either from local fields or from energed pupae.

Most of the eggs and larvae of Euploea core Cramer were collected from Shum Chun, China. Eggs were placed in a glass container covered with a petri dish. Newly hatched larvae were reared either in plastic container or petri dish. Third instar larvae were transferred with a brush to oleander (Nerium indicum Mill.) or fig foliage (Ficus sp.) which were placed in a bottle of water so as to be kept fresh. Fully grown larvae, when attached themselves to the leaves, were placed separately in a vial and allowed to pupate. Adults were obtained from local fields or from laboratory reared pupae.

All observations were made on freshly dissected materials in insect saline. The size of gut regions were measured with a micrometer under a low power stereo microscope.

OBSERVATIONS

The gross morphology of the gut of these two species is essentially the same. The larval gut, similar to other Lepidopterous larvae (Gray, 1931; Henson, 1931, 1932; Chauthani and Callahan, 1967; Judy and Gilbert, 1969; Chi et al., 1975), is more or less a simple straight tube leading from the mouth to the anus. Alterations of corresponding regions of the gut of the two species during metamorphosis are more or less the same.

According to embryonic origin, the gut of both species can be divided into three main regions, namely the foregut, the midgut and the hindgut.

I. FOREGUT

1. Active feeding fifth instar larva (Fig. 1):

The foregut is the first region of the three main divisions of the entire alimentary canal containing the buccal cavity, pharynx, oesophagus, crop and the oesophageal invagination or known as the stomodeal valve. It is located immediately behind the mouthparts and extends to the third thoracic segment of the insect.

The mouth is the anterior opening of the alimentary canal and it originates behind the paired mandibles. Extends posteriorly to the body about 0.6-1 mm is the funnel-shaped buccal cavity which tapers to join the pharynx. At the junction where the buccal cavity meets the pharynx, there are several strong circular muscles which are probably concerned with the ingestion of food.

No immediate distinction marks the junction where the pharynx joins the oesophagus. However, the oesophagus is characterized by having numerous surrounding circular muscle bands as well as dorsolateral and ventrolateral dilator muscles which insert to its walls. The musculature of the cephalic region of the foregut is similar to those described by Henson (1931), Snodgrass (1935), Chauthani and Callahan (1967), and Judy and Gilbert (1969) in other Lepidopterous larvae.

The buccal cavity is flexed ventrad, but the pharynx and oesophagus assume a more horizontal position in the head. Before joining the crop in the thorax, the posterior part of the oesophagus expands slightly. However, the crop can be viewed as an expanded portion of the oesophagus.

The crop follows the oesophagus which terminates approximately at the posterior margin of the head and joins the midgut at the third thoracic segment. The size of the crop varies from 3.3 to 4.5 mm in Euploea, and from 4.7 to 5.5 mm in Erionota, depending on the quantity of food present in the lumen. The crop is covered by a regularly spaced muscle network which is made of inner longitudinal muscles and outer circular muscles. This network enables the crop to expand twice its capacity to store the ingested food when needed. However, in an active feeding larva, the crop is generally filled with food clippings.

Located at the posterior foregut and extended to the anterior midgut is the oesophageal invagination or the stomodeal valve. It is composed of 3 leaflets. Each leaflet has 6-7 fingerlike projections at the tip (Fig. 2).

No marked difference of the gross morphology of the foregut of Erionota and Euploea is noticeable except the foregut in Erionota is slightly longer than the corresponding regions in Euploea.

2. Prepupal stage:

The fifth instar of Erionota lasts about 9 days

while that of Euploea lasts 7-8 days. The first 4-5 days are feeding stage as previous instars. In most cases, the larva ceases feeding three days prior to pupation, and then gradually voids its gut contents. In general, cease of feeding marks the beginning of larva-pupa transformation. However, it takes approximately two days to empty all the contents in the gut.

In the prepupal stage, the crop of both species begins to reduce in diameter immediately after emptying the contents to the midgut. Gradually, the crop becomes a narrow tube with numerous longitudinal folds or creases. The cause of such a reduction of size is attributed to the contraction of circular muscles (Judy and Gilbert, 1969). Eventually, the crop becomes reduced to a narrow tube of uniform diameter.

Before pupal ecdysis, the oesophageal invagination is withdrawn from the anterior midgut to the posterior foregut (see p. 47-48).

3. Pupal stages:

Dissection of 0-hr-pupa reveals that no apparent changes occured except the reduction of the diameter of the

foregut (Fig. 3) and the shortening of the oesophageal invagination. The diameter of the foregut has now reduced ½ to 1/3 of its original size. It is now covered by a thin layer of evenly distributed fat and connective tissue or confuse tissue. The oesophageal invagination has been withdrawn from the midgut forming an opaqe "plug" which occludes the lumen of the posterior margin of the crop. The alignment of the oesophagus is attributed to the contraction of the outer lying muscular connective (Bahadur and Kathuria, 1971).

In a 35-hr-pupa of Euploea, the diameter of most of the foregut has reduced from 0.5 mm to 0.3 mm except the posterior margin, where the withdrew larval oesophageal invagination is located, remains about 0.7-0.8 mm. Furthermore, on the dorsal side of this margin, a slight evagination or swelling is formed, which is the developing adult crop. However, no evagination is found on the foregut of a 35-hr-pupa of Erionota.

In a 45-hr-pupa, the cuticular intima of the foregut sloughs from the epithelium and occludes the lumen like a thread (Fig. 4). At the same time, the foregut is more delicate

than before. This is attributed to the disintegration of the outer-lying musculature which forms the skeleton of the foregut. In the pupa of Erionota, a tiny evagination is found forming on the dorsal side of the posterior foregut. It is obvious that the timing of the development of the adult crop varies in these two species.

As a result of cell division, the developing adult crop in a 80-hr-pupa of both species increases in size rapidly. The developing crop of Erionota is more or less triangular in shape while that of Euploea is barrel-shaped. The crop is transparent and is filled with clear fluid.

By the time the pupa is 100-hr old, the developing crop of Erionota and that of Euploea increase 2 fold and 4 times respectively.

At the base of the developing crop just before joining the midgut, the posterior foregut expands slightly to form the proventriculus.

In a 150-hr-pupa, no further changes of both species are noticeable except the enlargement of the developing crop (Fig. 4). The posterior part of the foregut left after the

formation of the developing crop is called the proventriculus. The proventriculus is noticeable only after the adult crop has well developed.

Once the developing crop obtained a steady size, the pupal development of the foregut is almost completed except the folding of the invagination of the proventriculus into the midgut to form the adult oesophageal invagination.

4. Adult:

The anterior foregut of an adult is only a simple straight tube with no diverticulum or projection, it remains narrow and unspecialized in the nectar-feeding adult.

Dissection of fresh adult emerged shortly after ecdysis reveals that the crop is inflated with gas. It is obvious that the inflation of the crop takes place during the expansion of the wings. However, after the inflation, the crop then looks like a silvery balloon occupying the upper part of the first thoracic segment, and in some cases, extends to the second thoracic segment. The crop has very strong peristaltic movements which is said to provide a compensatory mechanism for maintaining haemocoel volume during the expansion of the wings (Judy and Gilbert, 1969).

II. MIDGUT

1. Active feeding fifth instar larva:

The midgut is the largest organ, located from the third thoracic segment to the sixth abdominal segment, occupying most of the space of the haemocoel, with three Malpighian tubules running along each side (Fig. 1).

The midgut of both species, unlike some other Lepidopterous larvae (Gray 1931; Judy and Gilbert, 1969; Chi et al., 1975), is only a straight tube without any diverticulum or caeca-like protuberance. However, similar to other insects, it is endodermal originated.

The midgut is a continuation which receives the foregut at the posterior margin of the third thoracic segment and leads to the pylorus of the hindgut at the sixth abdominal segment. No musculature is found holding the midgut in place but the tracheae.

The midgut of an active feeding 5th larva is characterized by its strong, active appearance. It is, in general, always filled with food clippings. The walls of the anterior midgut as well as that of the posterior midgut almost always have circular creases. This is

attributed to the strong muscle contraction which is probably responsible for the receiving of food clippings from the crop and the removal of food pellets into the hindgut. It is obvious that the contraction of both longitudinal muscles and circular muscles constructs the so-called peristalsis which makes the rhythmic transport possible. Reverse of those of the ectodermal originated foregut and hindgut, the arrangement of the longitudinal muscles of the midgut are external to the circular muscles. There are distinct pairs of longitudinal muscle bands running along the midlines of the dorsal and ventral area of the midgut, one pair on each side.

Enclosing all the food clippings, a transparent membrane lines beneath the epithelium along the entire midgut, this is known as the peritrophic membrane. However, the membrane may be multi-layered in the posterior half of the midgut.

2. Prepupal stage:

The midgut undergoes metamorphic changes early before all food contents are removed. However, the cease of feeding can be regarded as the beginning of the larva-pupa transformation.

After the removal of food contents to the ileum, the midgut is less rigid and begins to reduce in diameter. However, instead of food clippings, it is now fully filled with clear liquid (Fig. 3).

Before pupation takes place, the midgut sloughs the larval epithelium to the lumen forming the orange coloured yellow body (see p. 57-58). The entire midgut is replaced by the pupal epithelium.

3. Pupal stages:

No further changes of the midgut are noticeable in a new pupa. The musculature shows no degeneration, and the midgut is therefore the most strong part of the entire alimentary canal during the larva-pupa transformation (Fig. 3).

In both Erionota and Euploea, the midgut shows no further metamorphic changes except the reduction of size. The midgut of Erionota persists as a narrow tube ca. 10 mm long and 1.5 mm diameter throughout the remainder of the pupal life. The midgut of Euploea, however, reduces gradually until it reaches a length of 5 mm.

In a 80-hr-pupa of Euploea, the lumen contains less liquid than before, and the yellow body (see p. 57-58)

is closely packed, thus, making the midgut hard and rigid. By the time the pupa reaches 100-hr or even 150-hr, the yellow body is, so far from being delicate, very hard indeed. However, in a 180-hr-pupa or 200-hr-pupa, it becomes softened. This is attributed to the gradual completion of the digestion of the yellow body by the pupal epithelium. In Erionota, the yellow body is always loosely packed in almost every stage, and is therefore more delicate in appearance.

The midgut empties its contents to the hindgut after the breaking down of the yellow body is completed. Furthermore, the discharge of wastes from the midgut to the hindgut can be regarded as the end of the metamorphosis of the midgut.

4. Adult:

The midgut of an adult butterfly is similar to that of the mature pupa, no immediate differences are noticeable except that the epithelial wall is much folded circularly.

III. HINDGUT:

1. Active feeding fifth instar larva:

The midgut of the active feeding 5th larva of

Erionota and Euploea is essentially the same. It consists of three regions: the pylorus, the ileum, and the rectum. The larval hindgut occupies most of the haemocoel from the 7th abdominal segment to the rear end of the insect.

The junction of the midgut and the pylorus is not immediately obvious since the diameter of the posterior imaginal ring is more or less the same as that of the posterior midgut. However, the musculature of the midgut terminates at the junction immediately before the posterior imaginal ring so that the epithelium of the pylorus is not as folded as the posterior midgut. The musculature of the hindgut of Erionota and Euploea agrees the descriptions of Reinecke et al (1973) for Manduca sexta.

The pylorus is subdivided into three regions: the posterior imaginal ring, the pyloric cone, and the pyloric valve (see p. 62-63). The thin walled pyloric cone tapers to join the pyloric valve about 1.5-2 mm posterior to the midgut. A pair of common Malpighian ducts inserts to the anterior edge of the pyloric valve. Each duct extends forward to form the enlarged common Malpighian ampulla which receives products from three Malpighian tubules. After running forward along

the midgut about two third the length of the midgut, the tubules turn back sharply and, again, running along the midgut to the hindgut. At the anterior rectal sac, the tubules insert to the rectum and form the cryptonephidial system (Fig. 1).

The pyloric valve or known as the pyloric sphincter is a heavily muscled tube which is situated between the pyloric cone and the ileum. This tube serves as a sphincter which regulates the passing of faecal pallets.

Posterior to the pyloric valve, the hindgut forms the expansible ileum in the 8th abdominal segment. In some other Lepidopterous larvae such as Manduca sexta (Reinecke et al., 1973) and Hyalophora cecropia (Judy and Gilbert 1969), the enlarge ileum is apparently different from the colon by their size and shape. In the case of Erionota and Euploea, it is a morphologically undifferentiated tube connecting the pylorus to the rectum. The ileum are surrounded by numerous circular muscles. The epithelium of the anterior end of the ileum is highly convoluted forming several longitudinal foldings which occlude the lumen.

The rectum follows the ileum at the anterior margin of the 9th abdominal segment. It is a large sac that occupies most of the haemocoel of the 9th and 10th abdominal segments. The rectum consists of the rectal valve and the rectal sac. The rectal valve, similar to the pyloric sphincter, is heavily muscled.

The rectum receives the insertion of the three pairs of Malpighian tubules which penetrate the outer and inner perinephric membrane of the rectum approximately 1 mm posterior to the rectal valve. After penetrating the outer perinephric membrane, the Malpighian tubules extend posteriorly beneath the outer space to the posterior part of the rectum and pass inward through the double-layered medial space, and extend forward. In the inner space, the tubules are called inner tubules which is extremely convoluted and difficult to trace. Eventually, the inner tubes terminate between the rectal epithelium and the inner membrane.

No rectal complex is found at the posterior end of the rectum, about 0.5 mm anterior to the anus. The region is known as the anal duct. Posterior to the duct is the anus which is the posterior opening of the alimentary canal (Fig. 5).

Again, no differences are noticeable in the gross morphology of the larval hindgut of Erionota and Euploea.

2. Prepupal stage:

After the completion of the removal of faecal pellets approximately 48 hours before pupation, the hindgut undergoes larva-pupa transformation. Similar to the metamorphic changes that take place in the foregut during prepupal stage, the hindgut reduces in length and diameter and gradually becomes a narrow tube. The peritrophic membrane, together with food contents, is voided into the hindgut.

3. Pupal stages:

In most cases, the hindgut of a newly pupated pupa is surrounded by a thick mass of the condensed muscles. Similar to the foregut, the musculature of the hindgut undergoes degeneration during metamorphosis. However, the association of the cryptonephric system and the hindgut remains in the same situation. The hindgut is flexed ventrally and is shortened considerably when pupation is completed. The shortening of the hindgut is largely a result of the contraction of the musculature. Furthermore, the withdrawal of the larval pylorus is a minor factor that results in the shortening of the larval pyloric cone. As

a result of the contraction of the pyloric cone, the common Malpighian ducts enter the pupal ileum immediately after the posterior imaginal ring.

In the early pupal stage, the hindgut is covered by a layer of evenly distributed diffuse tissue which is made up of degenerating muscles, fat bodies and Malpighian tubules of the cryptonephric system. Although the junction between the ileum and the rectum is no longer noticeable, the larval rectal valve is recognizable in terms of the insertion of the Malpighian tubules to the rectum.

The hindgut begins to elongate by means of cell division at about 45 hours after pupation (Fig. 4). In many cases, the remnants of the degenerating muscles of the larval ileum spread into the haemocoel, thus, making the appearance of the hindgut fuzzy. This phenomenon indicates the disintegration of the cryptonephric system and the reformation of the larval fat bodies. However, the hindgut becomes a slender narrow tube of nearly uniform diameter.

With the elongation of the pupal ileum, the posterior hindgut expands to form the rectal pouch (rectal proper). The rectal caecum is a diverticulum anterior to the rectal

pouch. It projects forward over the insertion of the ileum, and develops after the rectal pouch has swollen (Fig. 4).

By the time the pupa is 100-hr old, the walls of the rectal pouch contain numerous small, round thickenings which are the developing rectal pads (Fig. 4). The majority are located in the posterior portion of the rectal pouch. However, none of these pads has been found in the rectal duct or the anterior part of the rectal caecum. The rectal proper tapers to join the rectal duct which is a simple tube leading to the opening of the rear end of the alimentary canal, the anus (Fig. 4).

As a result of elongation, the pupal ileum is coiled between the midgut and the rectum (Fig. 5). However, no further morphological changes are noticeable.

In a 200-hr-pupa, the midgut empties its contents into the ileum. By the active actions of peristalsis of the ileum, excreta from the midgut as well as the Malpighian tubules are discarded to the rectum which serves as a storage chamber.

The discharge of meconium to the hindgut indicates the completion of pupal development of the alimentary canal.

4. Adult:

Shortly after adult ecdysis, the insect releases the meconium from the rectum. No further morphological changes are noticeable in the hindgut of adult.

Fig. 7 gives a summary of the larva-pupa-adult transformations.

Fig. 1 Diagrammatic representation of the larval guts of Erionota (A) and Euploea (B) at active feeding stage.

cr : crop

il : ileum

lm : longitudinal muscles

mg : midgut

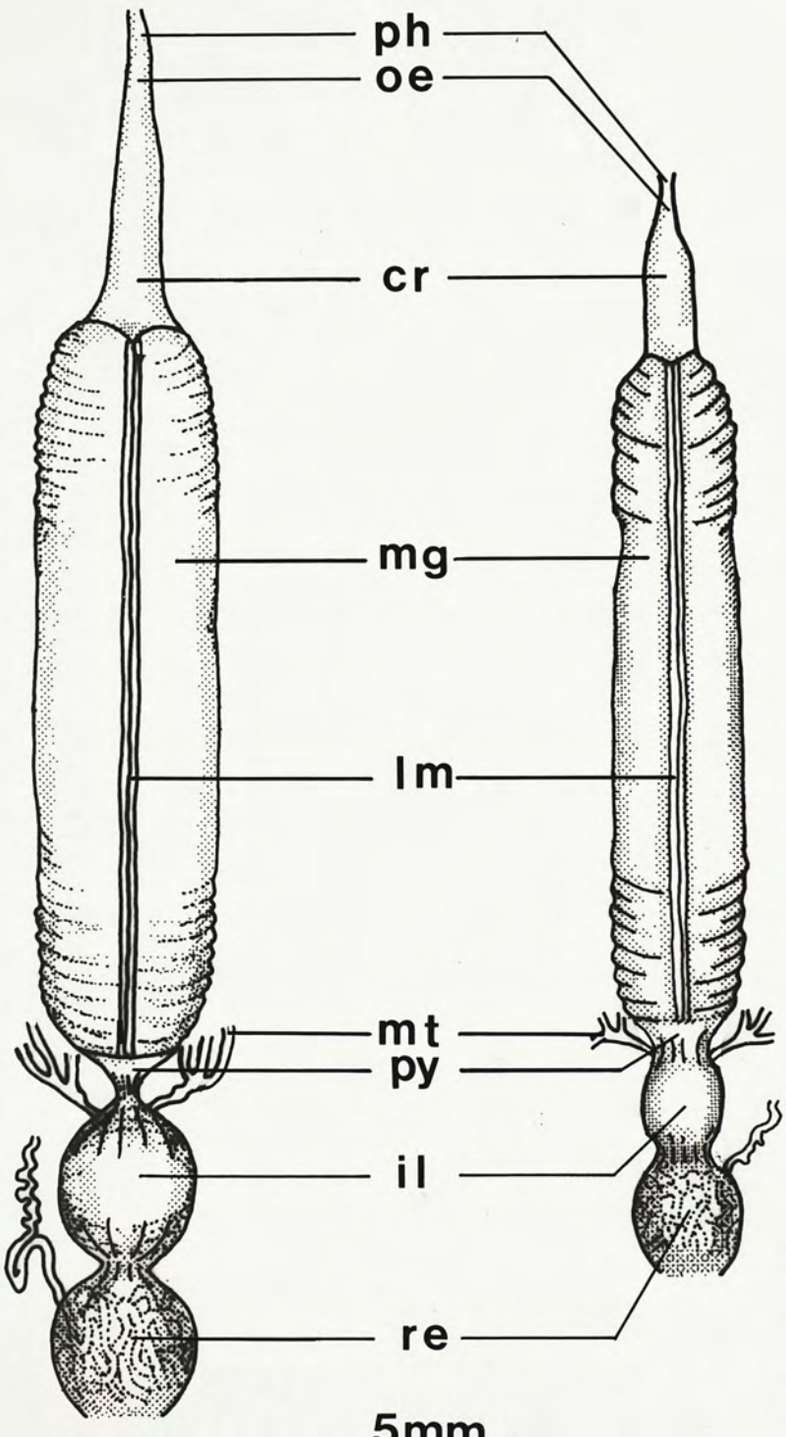
mt : Malpighian tubules

oe : oesophagus

ph : pharynx

py : pylorus

re : rectum



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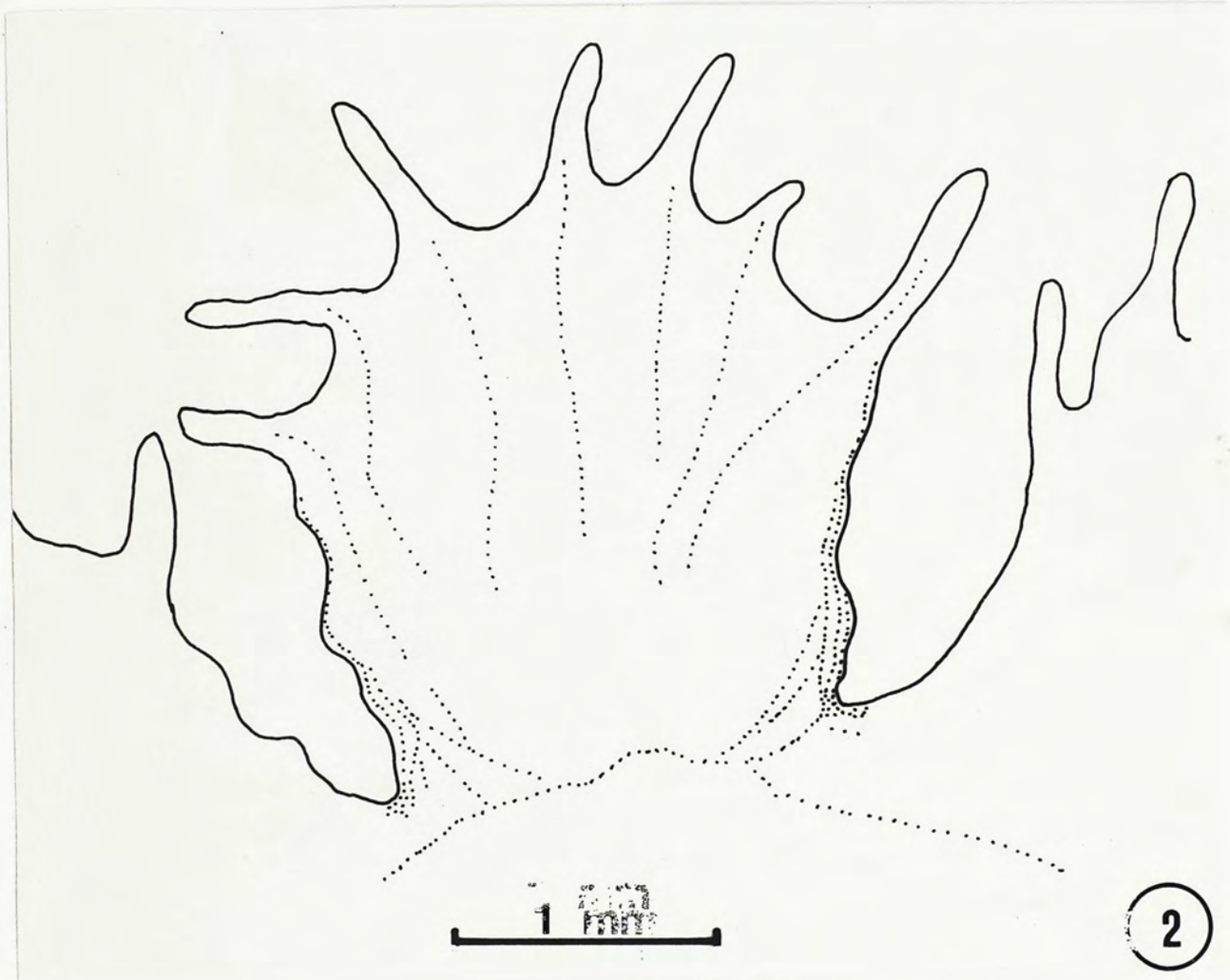

Fig. 2 Diagrammatic representation of one of the three leaflets of the stomodeal valve of Erionota at active feeding stage.

Fig. 3 Diagrammatic representation of the pupal guts of Erionota (A) and Euploea (B) at 0-hr. Note the diffuse tissue (arrowed) of the rectum.

fg : foregut

mg : midgut

hg : hindgut

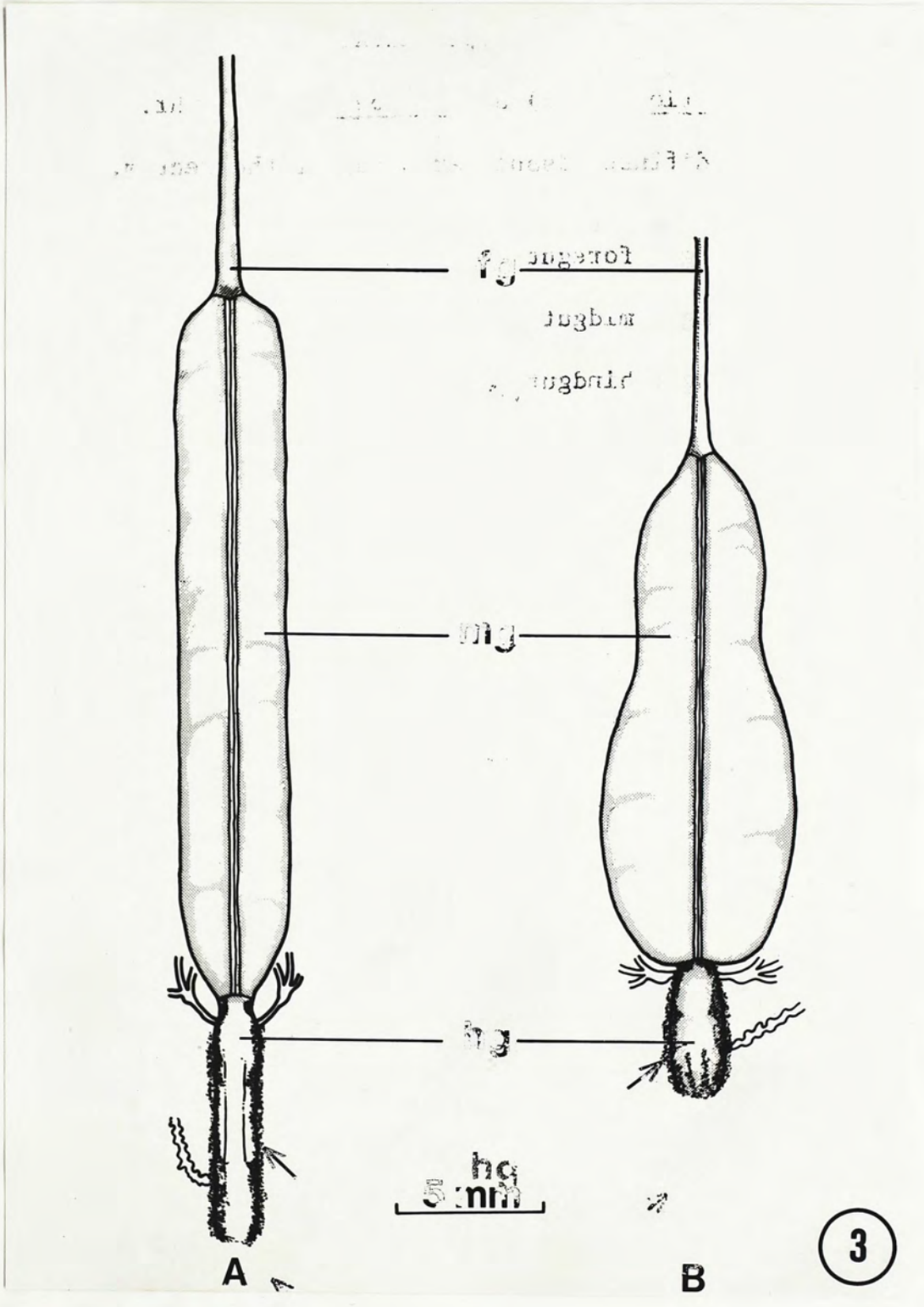

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Fig. 4 Diagrammatic representation of the pupal guts of Erionota (A) and Euploea (B) at 150-hr.

ci : cuticular intima

cr : crop

fg : foregut

il : ileum

mg : midgut

re : rectal caecum

rd : rectal duct

rp : rectal pad

rs : rectal sac

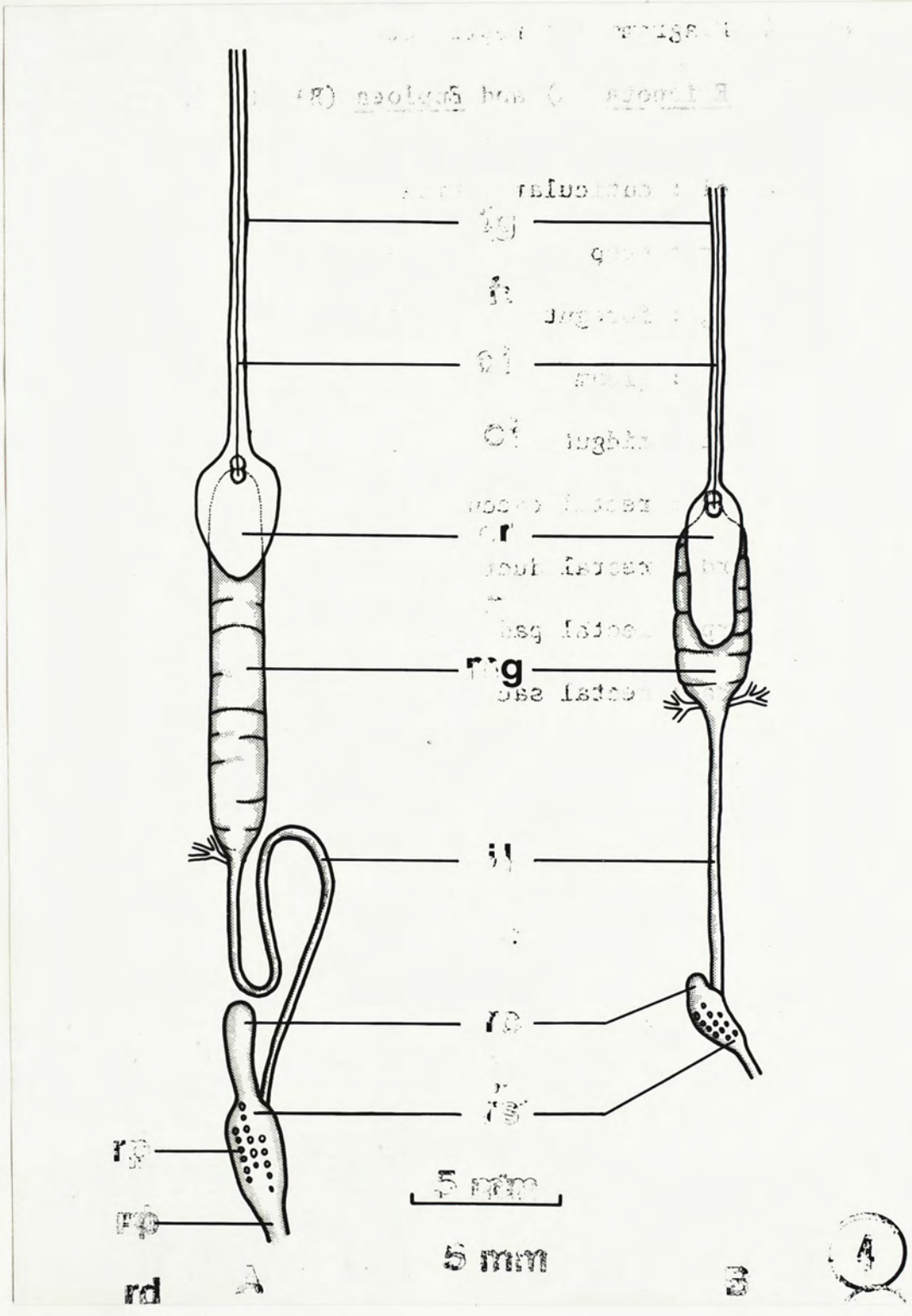
rg
rr
rrg
rp
rs
rp
rd
5 mm
5 mm
A
B
4

Fig. 5 Diagrammatic representation of the pupal guts of Erionota (A) and Euploea (B) at 250-hr. Lateral views of the crop are shown on the left hand side of respective species.

cr : crop

fg : foregut

il : ileum

mg : midgut

rc : rectal caecum

rd : rectal duct

rs : rectal sac

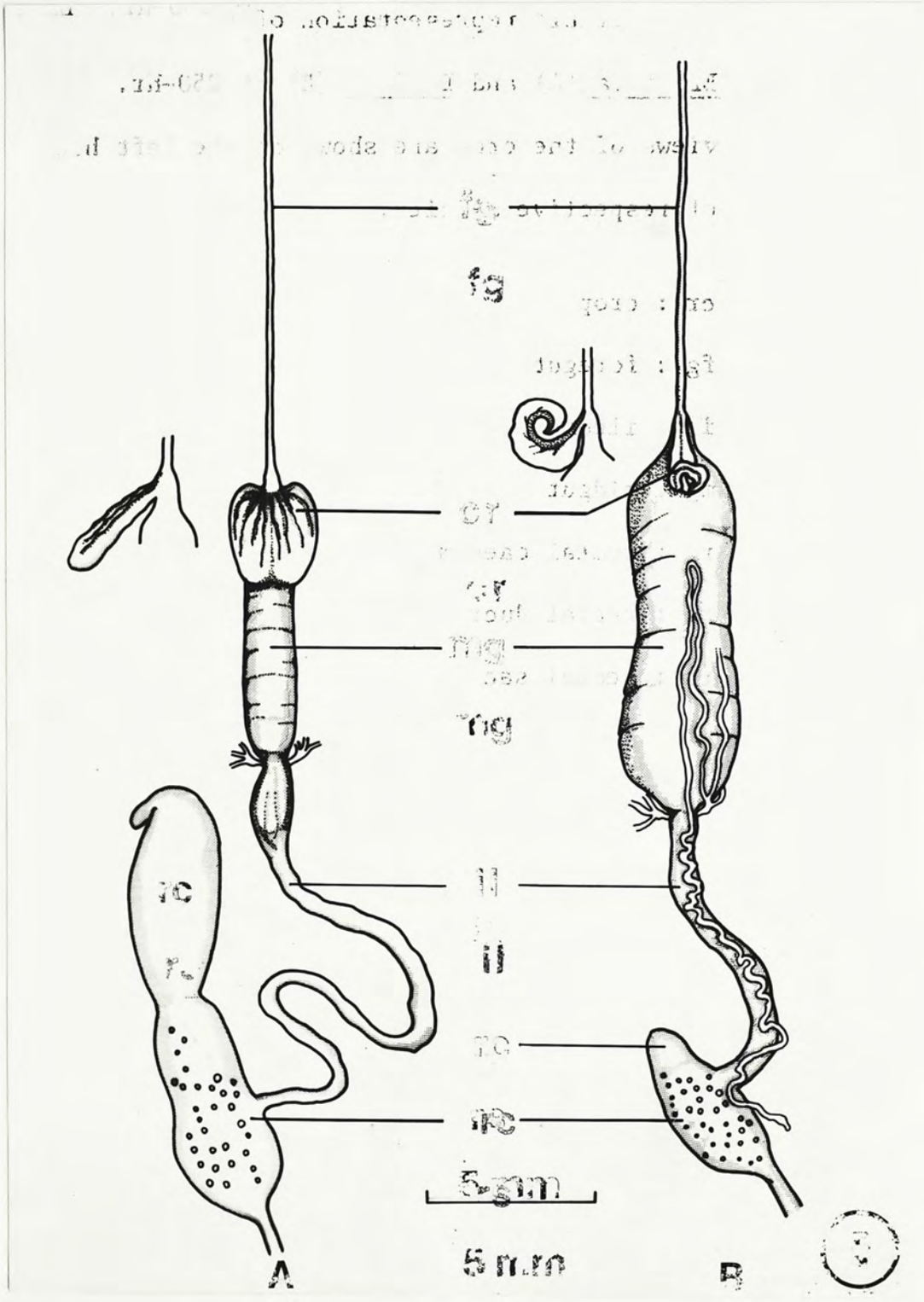
5 mm
A
B

Fig. 6 Diagrammatic representation of the adult guts of Erionota (A) and Euploea (B).

cr : crop

fg : foregut

il : ileum

mg : midgut

pv : proventriculus

re : rectum

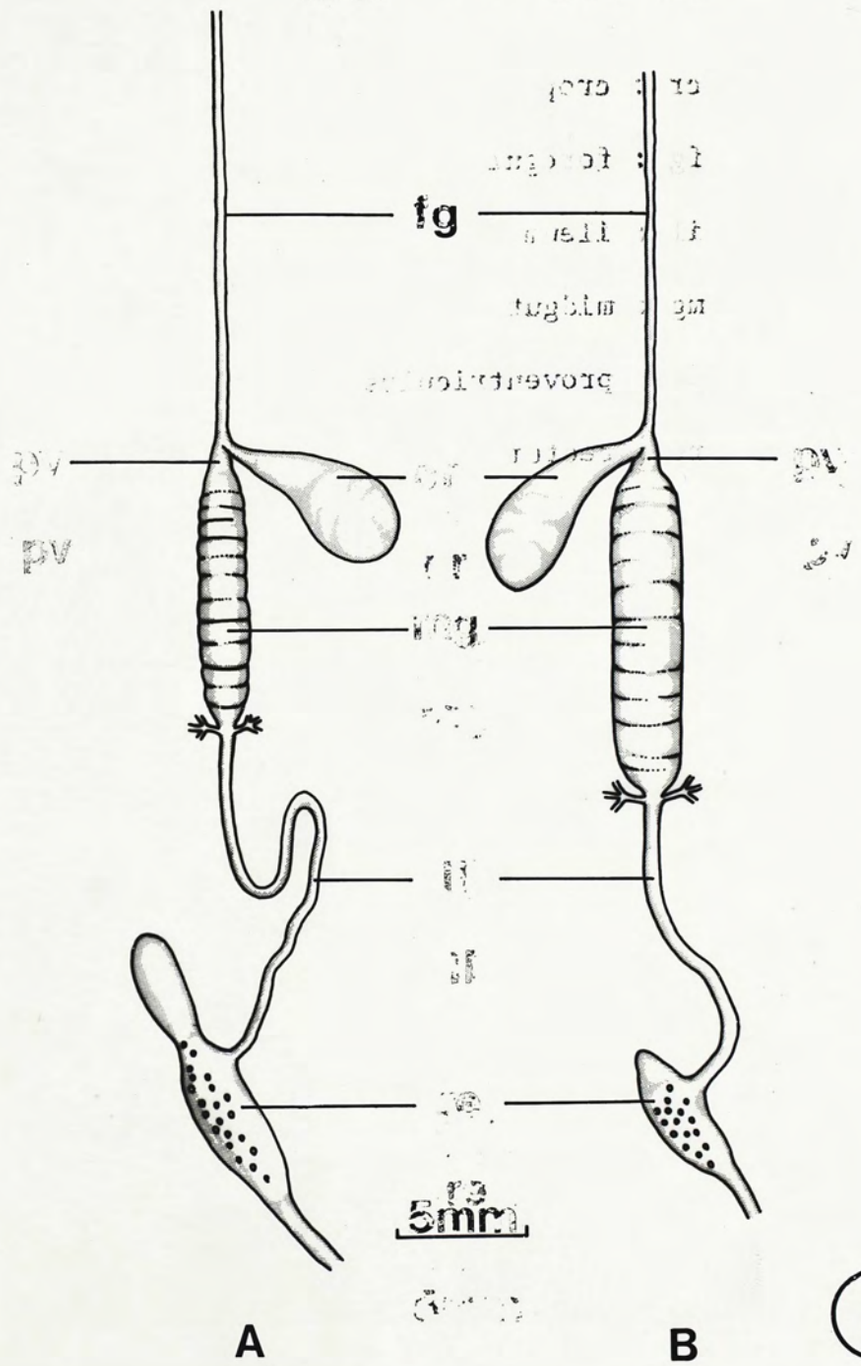

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Fig. 7 Diagrammatic representation of larval, pupal, and adult guts - a summary of the transformations.

cr : crop

fg : foregut

il : ileum

mg : midgut

pv : proventriculus

re : rectum

PART II

HISTOLOGY OF THE GUT OF *ERIONOTA* AND *EUPLOEA* DURING METAMORPHOSIS

INTRODUCTION

Studies on the internal anatomy of Lepidopterous larvae in relation to metamorphosis probably began with the classical works of Malpighi (1669) and Swammerdam (1685). Following the observations of these pioneers, Lyonnet (1962) contributed a monograph on larval structures of the goat moth caterpillar. Bordas (1911) produced a comparative investigation of the gross and histological structures of the digestive tract and malpighian tubules of more than two dozen larvae selected from varies Lepidopterous families. Numerous articles have been contributed after the investigation of Bordas (1911).

Peterson (1912) investigated the internal anatomy of the tomato hornworm, Protoparce quinquemaculata, in detail. The larval alimentary canal of the milkweed butterfly, Vanessa urtica and that of the large white, Pieris brassicae have been extensively studied by Henson in 1931 and 1932 respectively. Henson (1931) gave a very detailed description of the larval alimentary canal both in gross morphology and histology. He regarded the anterior imaginal ring as the anterior interstitial ring, for the reason "because it is present in essentially similar form in both the larva and imago. It plays so little in the metamorphosis that it can scarcely be

regarded as an embryonic region set aside for the production of imaginal tissues." However, he gave a very detailed description of the larval foregut and the hindgut. In 1932, he reported the embryonic development of Pieris brassicae, which was, again, a detailed investigation. Neiswander (1935) studied the gut of the oriental fruit moth larva. The midgut of the silkworm, Bombyx mori has been extensively investigated by Shinoda (1926), Machida (1933) and Tsujita (1943, 1948).

In the past 30 years, the study of the gut of Lepidopterous larvae became more popular. El-Sawaf (1950) studied the gut of the wax moth, Galleria mellonella. Drecktrah et al (1966) contributed a very detailed anatomy and morphology of the European corn borer, Ostrimia nubilalis.

In the 1960's and 1970's, various authors have concentrated in the ultrastructure of certain organs or structures of the Lepidopterous alimentary canal (Durr, 1967; Mcleod et al., 1969; Byers and Bond, 1971; Reinecke et al., 1973; Chi et al., 1975; Schultz and Jungreis, 1977). However, works on the adult or post-embryonic development of the gut of Lepidoptera are few (Verson, 1905; Gray, 1931; Krishnakumaran and Schneiderman, 1964; Chauthani and Callahan,

1967; Judy and Gilbert, 1969, 1970; Waku and Sumimoto, 1971, 1974). A few accounts are reported on the development of the Malpighian tubules of Lepidoptera and their associated structure (Srivastava and Khare, 1966; Khare, 1974). However, most of these works are done on moths and are restricted on larvae. There is a paucity of detailed information on the functional morphology of the gut of butterflies during metamorphosis.

MATERIALS AND METHODS

Insects were dissected in insect saline. The gut was either fixed in Formal saline or Bouin's fluid. Tissues were dehydrated in ascending series of alcohols and embedded in paraffin at 56°C. Sections were cut at 3 μ - 7 μ and were stained with Erlich's Hematoxylin or Delafield's hematoxylin counterstained with eosin. However, PAS test was used in some cases (Pearse, 1968).

OBSERVATIONS

I. FOREGUT:

1. Active feeding 5th instar larva:

The foregut is the first division of the three main

divisions of the entire alimentary canal, containing the buccal cavity, the pharynx, the oesophagus, and the thin-wall crop which are ectodermal in origin (Fig. 1).

a. Buccal cavity:

The buccal cavity is the anterior end of the foregut. The epithelium of the cavity is composed of squamous cells. The intima lining the epithelium of the cavity is approximately 5-7 μ thick and bears numerous rows of posteriorly directed spines that are about 4-5 μ long. Several dilator muscles and longitudinal muscles insert to the walls of the buccal cavity. These strong muscle bands are concerned with the ingestion of food.

b. Pharynx:

The pharynx is a continuation of the buccal cavity leading to the oesophagus. Similar to that of the buccal cavity, the epithelium of the pharynx is composed of squamous cells with centrally located, ovoid nuclei and is lined with thick spiculated intima as well (Fig. 8). Unlike the epithelium of the buccal cavity, the epithelium of the pharynx is much folded, forming an occluding and expansible tube.

c. Oesophagus:

Leading inward from the pharynx is the oesophagus which is formed by an epithelium lined with smooth intima that varies in thickness (8-25 μ) (Fig. 9). There are also a number of protrusions formed by the folded epithelium enabling the oesophagus to expand during ingestion of food. The muscles of the oesophagus are quite different from that of the pharynx. Adhering to the epithelium, there are 20-25 circular muscle bands with a few externally lined longitudinal muscles which insert to the epithelium of the anterior end of the oesophagus.

d. Crop:

The crop is a thin-walled dilation of the oesophagus. The epithelium of the crop is formed of squamous cells lining with a thin cuticle. The epithelial cells generally possess more or less fattened ovoid nuclei. There are lots of mini creases on the crop wall; the nuclei appear discoidal or branched. The epithelium extends to the anterior midgut and forms the oesophaeal invagination.

e. Oesophageal invagination:

The oesophagueal invagination splits into three leaflets (Fig. 2) which extend to the lumen of the anterior

midgut. These leaflets are double-layered. Located between these layers are several circular muscles or annular muscles and tracheae. Longitudinal muscle bands are found attached on the external side of the oesophageal invagination to the rim of the anterior midgut. According to Romoser and Venord (1967), Bahadur and Kathuria (1971), the oesophageal invagination can be subdivided into five regions (Fig. 15a, 16).

The first region is situated at the junction between the foregut and the midgut. The cells of this region are very small with centrally located ovoid nuclei. It is obvious that the cuticular intima of the foregut terminates here between these cells (Fig. 15a, 16).

Situated immediately anterior to the first region is the anterior imaginal ring or the second region. This region consists of embryonic cells which develop into several adult organs during metamorphosis.

The third region is made up of cells located below the annular muscles. The cells of this region are less closely appressed and can, therefore, be distinguished

easily. Moreover, the size of the cells of the third region are larger than those of the first and second regions (Fig. 15c).

The fourth and fifth regions are both composed of cells with large nuclei. Roughly, R4 and R5 consist of the cells of the posterior layer and anterior layer of the oesophageal invagination respectively (Fig. 15a).

2. Prepupal stage:

Immediately after the cease of feeding, the foregut voids all its contents to the midgut, and undergoes condensation. As a result of the contraction of circular muscles, the epithelium of the foregut folds longitudinally, thus occluding the lumen. However, the folds of the larval crop are more extensive and consist of both longitudinal and circular creases (Fig. 15b). The cuticular intima that lines the epithelium of the foregut now becomes detached gradually.

Despite the narrowing of the foregut, the most drastic change in the foregut during the prepupal stage is the alignment of the oesophageal invagination. The oesophageal invagination is withdrawn from the anterior midgut gradually. The intima of the foregut becomes more

distinct and loosely attached to the invagination; this is largely a result of the shortening of the valve. Prior to the pupal ecdysis, the valve is withdrawn completely from the midgut and is situated at the posterior foregut where it seals the lumen (Fig. 15b).

Dissections of the late 5th instar larva reveal that Region 2 and 3 are shortened and the number of cells in the regions is apparently increased. Cells of Region 4 and 5 are closely packed. The intima has detached from the epithelium and occluding the lumen.

3. Pupal stages:

a. Anterior foregut:

In a 0-hr-pupa, the epithelial wall of foregut is folded longitudinally. As a result of condensation, the diameter of the lumen is much reduced. The epithelial cells become more or less cuboidal. The thick intima is still lining the epithelium and the muscles remain intact (Fig. 10).

As the foregut undergoes further condensation, the epithelial cells become columnar. The intima is likely to be detached from the epithelium. By the 35-hr to

45-hr after pupation, the lumen is reopened and the epithelium is no longer folded (Fig. 12, 13). The epithelium is now composed of cuboidal cells with centrally located ovoid nuclei. The outerlying muscles undergo degeneration. In a 80-hr-pupa, the muscles are no longer evident, and the intima is sloughed to the lumen. The epithelial wall of the anterior foregut is now composed of more or less elongated squamous or cuboidal cells with comparatively larger nuclei (Fig. 14).

b. Posterior foregut:

In a 0-hr-pupa, the alignment of the oesophageal invagination has not yet completed. In Erionota, the alignment is completed at 35-hr after pupation (Fig. 17) while that in Euploea is much earlier - 24 hr (Fig. 20). After the completion of the alignment, the cells of each region are quite distinct. The cells of Region 4 and 5 are closely packed, with large and deeply staining nuclei (Fig. 17); those of the anterior imaginal ring are columnar with tiny nuclei which are closely appressed (Fig. 17, 20). However, the completion of the alignment can be regarded as the beginning of further development

of the anterior imaginal ring and the degeneration of Region 4 and 5.

In a 30-hr-pupa of Euploea and a 40-hr-pupa of Erionota, numerous mitotic figures can be seen at the anterior imaginal region - Region 2 (Fig. 21). By the 30-hr-pupa of both Erionota and Euploea, numerous darkly staining globular bodies are found in Region 4 and 5 and extend to the outerlying connective tissues (Fig. 22). According to Bahadur and Kathuria (1971), these globular bodies are formed by the cells of Region 4 and 5 after degeneration. Furthermore, these bodies are probably the pupal 'spherules', which are multinucleate masses that phagocytose larval fragments (Whitten, 1968). After the alignment has completed, the muscles surrounding the foregut are poorly defined. As the adult crop develops at about 25-hr after pupation, the muscles break into small fragments and undergo gradual degeneration (Fig. 20).

The development of the adult crop becomes obvious in the 45-hr-pupa of Erionota and the 35-hr-pupa of Euploea (Fig. 22). The degenerating cells of Region 4

and 5 and those of the outerlying muscles are seen by their darkly staining globular appearance.

The adult crop increases rapidly in size as a result of mitotic divisions. By the time the pupa is 100-hr old, the developing crop is enlarged 3 fold. The roof of the developing crop is composed of large cuboidal cells with large, centrally located nuclei (Fig. 18e, 18f). The floor, however, is composed of comparatively small cells. In a 200-hr-pupa, cytoplasmic projections are noticeable on the cells of the crop near the proventriculus (Fig. 28).

As previously stated, the anterior imaginal ring develops to form the adult crop in early pupal stage. The cells of the posterior region of the anterior imaginal ring left after the formation of the developing adult crop undergo further changes. The anterior 1/2 of this region of Erionota and the anterior 1/3 of Euploea become folded upon the anterior margin of the posterior region and gradually covers it as the pupa becomes 150-hr old (Fig. 18f). In Erionota, the invaginated anterior region and the posterior region consist of cuboidal cells at first and gradually become flattened

in a 220-hr-pupa (Fig. 18). As a result of flattening, the epithelium increases in length and becomes folded and projects to the lumen. The epithelial cells of the posterior region, however, are highly appressed (Fig. 18).

In contrast to this, the epithelial cells of the proventriculus of Euploea, both of the anterior and posterior regions, are more or less cuboidal in almost all stages. In a 220-hr-pupa, the epithelium of the region becomes flattened and, as a result, the epithelium is highly convoluted and compressed (Fig. 23, 24). Although the old intima is occluding the lumen of the foregut, a new one is formed lining the epithelium.

No further changes are noticeable hereafter and throughout the remainder of the pupal life except the regeneration of the muscles that surround the proventriculus. The proventiculus is, again, heavily muscled by the time the pupa is of 260-hr in Erionota and of 240-hr in Euploea respectively.

4. Adult:

Dissections of newly emerged adults (Fig. 19, 26)

reveal that the double layered posterior region has folded posteriorly into the lumen of the anterior midgut, forming the adult oesophageal invagination. The crop has squamous cells of large nuclei (Fig. 29).

II. MIDGUT

1. Active feeding 5th instar larva:

The midgut is a simple straight tube leading from the foregut to the hindgut. Unlike other parts of the alimentary canal, the midgut is endodermal originated.

As described by Snodgrass (1935) for Lepidoptera in general, the midgut epithelium consists of columnar cells, goblet cells and wedge-like regenerative cells lining along the basement membrane. All these cells are arranged in a single layer (Fig. 32).

The midgut can be roughly distinguished into three regions: the anterior midgut, the mid-midgut, and the posterior midgut.

a. Anterior midgut:

The anterior midgut is the anterior chamber where digestion of ingested food probably takes place. Columnar

cells and nearly equal number of goblet cells made up the single-layered, much folded epithelial wall (Fig. 30). Each cell has a fine brush border lining on the apical surface, and a large ovoid nucleus located in the apical half. The cytoplasm is granular in appearance. In many cases of Erionota, the nuclei are slightly flattened and are centrally located (Fig. 31).

The goblet cells are large and barrel-shaped. Each goblet cell also possesses brush border and has a large urn-shaped central cavity (Fig. 30). The ovoid nucleus is restricted to the basal end of the cell. The goblet cells are more abundant in the anterior midgut but fewer than those of the mid-midgut and posterior midgut.

The peritrophic membrane is formed by the delamination of the brush border to the lumen (Waterhouse, 1953; Smith, 1968; Wigglesworth, 1972) (Fig. 31). It is a structure probably functioning in preventing actual contact between the epithelium and ingested food (Wigglesworth, 1972) (Fig. 33).

b. Mid-midgut:

The epithelial wall of the mid-midgut is smooth, unfolded. The columnar cells of the mid-midgut are slightly larger than those of the anterior midgut. Each nucleus is placed centrally (Fig. 32)

The goblet cells are extremely abundant in the mid-midgut (Fig. 32). The contents of the central cavity has the same staining property as the cytoplasm which is eosinophilic. The nuclei are located near the basal end of the cells.

The peritrophic membrane of the anterior midgut is usually a single layer, but in the mid-midgut and the posterior midgut, it appears to be formed of several layers (Fig. 31).

c. Posterior midgut:

Similar to the anterior midgut, the epithelium of the posterior midgut is much folded. The goblet cells are extremely abundant. The columnar cells are more or less elongated with their nuclei located centrally (Fig. 33).

Numerous spherical bodies or vesicles are found lining along the brush border or located randomly in the

space between the epithelium and the peritrophic membrane (Fig. 33). Obviously, these vesicles are restricted in this space since none of them has been found in the lumen among food particles. These vesicles are probably formed by the protrusions of the epithelial cells (Fig. 33).

The regenerative cells are located beneath the basement membrane, interspersed among the tall cells (Fig. 32). The cells increase in number during maturation from instar to instar, and begin to grow at the beginning of resting stage forming a new epithelium for the pupa. These cells are smaller in comparison with the others of the epithelium, and are oval in shape having an ovoid nucleus located in the centre.

The peritrophic membrane of the posterior midgut extends to the pyloric cone of the hindgut, leading food particles to the pyloric valve.

Generally, there are circular muscles around the epithelium just beneath the basement membrane, and longitudinal muscles running externally.

2. Prepupal stage:

Most of the metamorphic changes of the midgut take place in this stage before pupation. After the larva has ceased feeding and has emptied the gut contents, the midgut begins to undergo larva-pupa transformation. Together with the food clippings, the peritrophic membrane is shed and discharged to the hindgut.

Due to the contraction of the longitudinal muscle and circular muscles, the epithelium of the midgut is highly folded circularily. The epithelial cells are appressed and elongates slightly as a result of the contraction. The goblet cells are flattened and are less distinct than they were. The central vacuoles are strongly eosinophilic (Fig. 34).

Regenerative cells become more conspicuous and more in number. In most cases, the striated border is no longer evident but the apical end of the epithelial cells consist numerous nucleated or non-nucleated vesicles (Fig. 34) which are probably the extrusions of the tall cells.

As the regenerative cells grow larger, small vacuoles enclosing a dark-green crystalline body are

noticeable (Fig. 34 arrowed). At this time, although the tall cells of the larval epithelium are appressed, distinction is noticeable between the two types of tall cells.

At about 12 hours after the midgut has voided all its contents, the number of regenerative cells is increased as a result of cell division. The tall cells are highly appressed and the extrusion of the tall cells becomes more distinct (Fig. 35). Gradually, the regenerative cells have enlarged further and now formed a continuous epithelium of columnar cells. The goblet cells and columnar cells have extended as slender fingers and the cytoplasm of this cell layer stains darkly with hematoxylin (Fig. 35).

Before pupation takes place, the larval epithelium is sloughed to the lumen (Fig. 36). The sloughed, highly folded epithelium stains heavily with hematoxylin in comparison with the newly formed pupal epithelium. The nuclei, however, are still evident as well as the larval brush border (Fig. 36). The apical end of the columnar epithelium of the newly pupated insect is irregular and lacks a definite surface. Numerous vesicles are seen in the lumen near the epithelium. These vesicles are probably discharged by the columnar cells in the 'apocrine'

way (Fig. 37). The cytoplasm of the columnar cells are obviously granular, with an ovoid nucleus located at the basal half of the cell (Fig. 37).

3. Pupal stages:

The outer lying muscular system persists intact and is applied to the basement membrane closely. Beneath the basement membrane, a cluster of new regenerative cells are formed and are located between the base of the tall cells. The shape, size and arrangement of the pupal epithelial cells vary between specimens. The distinction of the three subdivisions of the midgut as previously described for the larval epithelium are no longer evident. In most cases, the epithelium of the anterior portion of the pupal midgut and that of the posterior portion are highly folded and the columnar cells are highly appressed. However, in the mid-portion, the epithelium is slender and the cells are shorter (Fig. 37-38), and the cytoplasm is granular in appearance. In Erionota, a brush border is re-established along the apical surface of the epithelium. This border, at first instance, is rather smooth, but as the pupa reaches 50-hr, again, consists of numerous vesicles extruding from the columnar cells (Fig. 39). All these

vesicles are non-nucleated and is believed to be enzymatic secretions responsible for the decomposition of the larval midgut. As the pupa reaches 220-hr, the brush border restores its fine appearance, no secretory vesicles are normally noticeable (Fig. 40).

In Euploea, unlike that of Erionota, a fine, smooth brush border is re-established shortly after pupation. No distinct secretory vesicles at the apical surface of the epithelium are normally noticeable until the pupa is 175-hr old (Fig. 42). This brush border persists its vacuolated condition throughout the remainder of the pupal life (Fig. 43) but, however, restores a fine, smooth condition immediately after adult ecdysis (Fig. 52). This agrees with the hardness of the yellow body as described previously in p. 15.

During pupal stages, the columnar cells of the pupal epithelium of the two species are essentially similar. In most cases, however, the nuclei are restricted at the basal half of the cells in Erionota while that of Euploea are located in the central (Fig. 39, 40, 42, 43).

4. Adult:

The midgut of both Erionota and Euploea becomes

increasingly folded during the final stage of pupa-adult transformation. In newly emerged adults, the midgut is deeply folded. In Euploea, the columnar cells have ovoid nuclei located at the basal half of cells (Fig. 44). The epithelium is less folded in Erionota, and the epithelial cells are club-shaped with more or less elongated nuclei located in the centre (Fig. 41). Regenerative cell are found interspersed at the base of the tall cells. No distinct secretory vesicles are noticeable in the midgut lumen of the two species.

In newly emerged adult, no distinct peritrophic membrane can be seen. However, in old adult of Euploea, a distinct multi-layered peritrophic membrane is located in the middle of the lumen (Fig. 44). It is a tubular structure enclosing numerous granules.

This tubular peritrophic membrane is believed to be originated at the anterior midgut where the epithelium meets the stomodeal valve (Waterhouse, 1953). No tubular or any other type of peritrophic membrane is noticeable in the midgut of Erionota; this agrees with the findings of Waterhouse (1953).

III. HINDGUT

1. Active feeding 5th instar larva:

The hindgut consists of three regions: the pylorus, the ileum, and the rectum (Fig. 1).

a. Pylorus:

The pylorus is a funnel-shaped region leading from the midgut to the ileum. The pylorus can be subdivided into three regions, the posterior imaginal ring, the pyloric cone, and the pyloric valve (Reinecke et al., 1973).

i. Posterior imaginal ring:

This ring marks the anterior end of the hindgut (Fig. 45). At the anterior region of this ring, an epithelial protuberance is formed by a cluster of columnar cells. Like other parts of the hindgut, the pylorus is ectodermal originated, thus consisting of intima-producing epithelium. The epithelial cells of the ring produce two types of intima.

The region, starting from the border between posterior midgut and the pylorus to the anterior half of the epithelial protuberance is covered

with smooth intima while spiculated intima covers the posterior half of the protuberance to the pyloric cone (Fig. 45).

ii. Pyloric cone:

The pyloric cone is made up of squamous cells lined with cuticular intima, and both circular and longitudinal muscles (Fig. 45).

The more or less elongated epithelial cells are arranged in a single layer. Each cell forms a small 'lobe' extending to the pyloric lumen. A thick intima lines the apical border of the epithelium (Fig. 45).

iii. Pyloric valve:

Entering the pyloric valve, several longitudinal protrusions are found occluding the lumen in the posterior region of the pyloric cone when the valve is constricted (Fig. 46).

The epithelial cells of the valve are larger than that of the cone, and the cuticular intima is also much thicker (Fig. 47). In the posterior region of the pyloric valve prior to the ileum, the

epithelial wall is composed of small, more or less hexagonal cells with ovoid nuclei centrally located.

The intima is about 20-25 μ thick and contains numerous spines, which are arranged in rows, around the anterior end of the pyloric valve (Fig. 46).

The duct of the common Malpighian ampulla exists in the anterior region of the pyloric valve. This duct is a tube receiving products from the common Malpighian ampulla which is the combination of three Malpighian tubules.

Posterior to the common Malpighian ampulla exit ducts the sphincter of the pyloric valve is very muscular (Fig. 47). This sphincter is composed of circular, anastomosing muscle bands. Longitudinal muscle bands have also been found attached on the outermost layer of circular muscles, and are much smaller than the circular muscles.

b. Ileum:

Immediately leading from the pylorus is the ileum. In Erionota, the ileum is an undifferentiated tube connecting the pylorus and the rectum. The ileal

wall, which is slightly convoluted, consists of more or less squamous cells with spherical nuclei (Fig. 48). The intima lining the epithelium is not thick when compared with that of Euploea (Fig. 48, 49).

No ileonodes (giant epithelial cells) have been found in the ileum and therefore no 'thick' intima is produced (Judy and Gilbert, 1970; Reinecke et al., 1973).

In Euploea, no distinct differentiation is noticeable in the ileum and the colon (Fig. 50) except that in the region immediately posterior to the pyloric valve. The epithelial wall appears to be composed of large, squamous cells with comparatively thick intima (Fig. 49).

c. Rectum:

The major components of the rectum are the rectal valve and the rectal sac.

i. Rectal valve:

The rectal valve is actually the 2nd sphincter of the hindgut. This valve is heavily muscled and is responsible for the entry of faeces to the rectum.

ii. Rectal Sac:

The rectal sac is a sac-like organ which is

located immediately posterior to the sclerotized ring (Fig. 51).

Similar to other green-feeding Lepidopterous larvae (Saini, 1964), the rectal sac of both Erionota and Euploea consists of 'cryptonephric condition', which means that the distal end of the Malpighian tubules are closely applied to the rectum and enclosed with it in a special arrangement (Ramsay, 1976). The so called 'rectal complex' refers to the reassociation of the Malpighian tubules and the rectum (Fig. 1).

Like that of the rectum of Vanessa urticae described by Henson (1937), the rectal complex of the two species is composed of rectal epithelium lining with cuticular intima and convoluted Malpighian tubules (Fig. 52).

The anterior 6/8 of the rectal sac consists of only 'cryptonephric' epithelium while the posterior 1/8 of the rectal sac contains both cryptonephric epithelium and normal epithelium. The 1/8 left is the anal duct which is composed of normal epithelium only.

The structure of the rectal complex may be thought of as four cylinders, one with another, forming three spaces (Reinecke et al., 1973). The anterior end of these cylinders fuse with each other and insert to the sclerotized ring.

The whole sac is invested by a thin circular muscle sheet externally. After immediately entering this muscle sheet and the outer perinephric membrane, the rectal lead, which is a portion of the Malpighian tubules leading from the iliac complex to the rectal sac, forms a dilation that is called the outer tubule (Fig. 52). The chamber containing outer tubules is called the outer space. The outer tubule penetrates two thin membranes and the empty medial space; it then enters the inner space to form the inner tubule which is highly convoluted (Fig. 52).

Tracheae are found abundantly located among the inner tubules and are derived from 2 large tracheae entering the rectal sac ventro-laterally on the posterior half.

Transverse sections through the posterior part of the rectal sac reveal that there are two distinct parts of the epithelium. The cryptonephric epithelium is reassociated with tubules while the non-cryptonephric epithelium is of normal appearance (Fig. 53); this is to say that the cryptonephric epithelium, unlike the anterior region of the rectal sac where the entire epithelium is in a cryptonephric condition, is restricted to three areas and is interrupted by normal epithelium (Fig. 53).

In the cryptonephric condition, cuticular intima is detached from the epithelium forming a subcuticular space. Furthermore, on the epithelium is the perinephric space which is composed of three space separated by the outer, and two inner membranes (Fig. 52).

In the normal condition, the cuticular intima adheres to the epithelium, and no perinephric space is formed on the other side of the epithelium.

At the posterior region of the rectal sac near the anus, the entire epithelium is of 'normal' condition, no cryptonephric condition is noticeable here. This region is, therefore, called the anal duct. However, its epithelium is composed of aquamous cells with thick intima.

The anus is the opening of the rear end of the rectum marking the terminus of the alimentary canal. The anus is very muscular; this enables it to control the egestion of faecal pellets at more or less regular intervals.

2. Prepupal stage:

It is not surprising to find that the histological changes of the hindgut during prepupal stage are essentially similar to that of the foregut since both the foregut and hindgut are ectodermal originated.

The initial changes of the hindgut are noticeable after the defaecation of the larva. In general, the hindgut undergoes only condensation of cells before pupation takes place. As a result, the hindgut becomes reduced in length and diameter. As stated previously, most of the epithelial cells

that composed the hindgut are either cuboidal or squamous. Some of these cells, such as the cells of the pyloric cone which were slightly elongated and were loosely packed, are condensed particularly and appressed closely (Fig. 54).

The characteristics of the cells of the various regions of the larval hindgut are no longer evident. All the cells of the hindgut have become more or less cuboidal with large ovoid nuclei which stain darkly with hematoxylin. Not only the shape of the cells of the epithelium, but also the size are uniformed. The hindgut gradually becomes a simple straight tube surrounded by numerous compressed muscle bands which show no signs of degeneration so far. At this time, most of the muscles begin to lose their striation but the sarcolemma remains intact.

The cryptonephric condition of the hindgut persists throughout the larval life. However, the epithelial cells of the rectum becomes cuboidal in shape, and the intima is detached from the cells.

3. Pupal stages:

a. Anterior hindgut:

The posterior imaginal ring of the hindgut is

essentially similar to the anterior imaginal ring of the foregut except that the former forms a protuberance (Fig. 45) instead of a valve. However, the fate of the posterior imaginal ring is different from that of the anterior imaginal ring; the former plays so little in the reconstruction of the adult gut that it forms only the 'tissue plug' (Gray, 1931) (Fig. 54, 55) which poorly serves as a pyloric valve in the pupa with no apparent function. The tissue plug is a dense cluster of cells with small ovoid nuclei derived from the junction cells between the midgut and the hindgut (Fig. 54-57).

During the early pupal stage after pupation, the pylorus is withdrawn gradually from the hindgut forming a mass of tissues (Fig. 64) occluding the anterior end of the hindgut. In a 30-hr-pupa, the posterior imaginal ring begins to form the posterior tissue plug similar to that of the foregut. As a result of the withdrawal of the pyloric cone to the posterior midgut, the pyloric valve is now situated immediately behind the midgut posterior to the insertion of the Malpighian ampulla exit ducts. Darkly staining globular bodies

are found among the epithelial cells of the larval pyloric valve and extend to the larval ileal epithelium and their surrounding tissues. This is the beginning of the degeneration of the surrounding muscles (Fig. 55).

As the break down of the larval muscles continues in the 30-hr to 50-hr pupa, the sarcolemma becomes indistinct, and a large amount of haemocytes and spherules (Fig. 68) are found interspersed among the disintegrating muscles.

After pupation has completed, the larval intima that lines the epithelial wall becomes detached gradually. By the time of 40-hr after pupation, the intima is sloughed to the lumen. After the elongation of the ileum, most of the intima congregates at the anterior end of the hindgut and seals the pyloric lumen (Fig. 56).

In a 50-hr-pupa, numerous darkly staining globular bodies are found at the anterior portion of the hindgut. The outerlying muscles are no longer distinct but form the diffuse tissue which extrudes into the haemocoel (Fig. 55). However, the larval pyloric cone is no longer noticeable except a large amount of darkly

staining globular bodies. It is highly probable that, similar to the corresponding R4 & R5 of the anterior imaginal ring, the larval pyloric cone is degenerated during the early pupal stage.

With the degeneration of muscles, the ileal epithelium elongates rapidly by means of cell division (Fig. 58). Numerous mitotic figures are found along the ileal epithelium. This reveals that the pupal hindgut lacks a division centre, but the entire ileum is responsible for the reconstruction of the adult ileum. However, at this time, the ileum is composed of columnar or cuboidal cells. As cell division proceeds further, the epithelial cells become cuboidal with large, centrally located nuclei (Fig. 58).

In a 80-hr-pupa of Erionota, cross sections reveal that the ileal lumen has reopened and the ileal wall is more or less hexagonal and is composed of closely packed columnar cells. The circular muscles are intimately adhered to the epithelium. By the time the pupa is 240-hr old, the ileal wall consists of more or less squamous cells with thick intima (Fig. 61).

At this time, the ileum is longitudinally folded forming six to eight longitudinal grooves protruding to the lumen. However, six attach-points for the longitudinal muscles are noticeable (Fig. 61).

In contrast, the ileum of Euploea is much folded into the lumen irregularily as a result of the high mitotic activity. The infolding is much pronounced as the pupa reaches an age of 200-hr (Fig. 60). The epithelial cells congregate and form clusters of cells along the length of the ileum. This is probably due to the limitation of space in the compressed abdomen of the pupa of Euploea. However, this could be thought of that the infolding of the ileal wall is the way to increase the surface area for some specific purposes, say, reabsorption of water. In addition, the Malpighian tubules are closely adhered to the highly folded ileal wall.

Prior to the adult emergence, the lumen of the ileum is opened wide to receive the meconium voided from the midgut. As a result, the ileal wall is less, but irregularily, folded. This is particularly true

in the anterior ileum posterior to the insertion of the common Malpighian ampulla exis duct, the diameter of the lumen has increased 2-3 fold.

b. Rectum:

The rectum, during larva-pupa transformation, is reduced to a tubular chamber. The anterior portion of the rectum is simply an oval ring of cuboidal cells with the old larval intima occluding the lumen. In the transverse section of the posterior region, the lumen is compressed to form three longitudinal folds that appear as diverticula (Fig. 65).

The intima is sloughed to the lumen, the subcuticular space as well as other spaces of the larval cryptonephric system are no longer evident (Fig. 62). The rectal epithelium is composed of a simple layer of cuboidal cells. In many of these cells, the nuclei are spherical while in others are slightly elongated as a result of the condensation.

Spherical vesicles or spherules, which stain darkly with hematoxylin, are found among the epithelial cells of the rectum in a 30-hr-pupa. Apparently, spherules are most abundant as the pupa reaches 45-hr of age (Fig. 68).

At this time, the degeneration of the outerlying muscles has been almost completed. The lumen of the rectum is now reopened. The epithelium is made up of columnar cells with large nuclei located in the central (Fig. 69). The rectum is swollen as a slender ballon known as the rectal proper. The rectum is free from the cryptonephric system, and the reassociation with Malpighian tubules is terminated.

Shortly after the reopening of the lumen and the completion of deassociation of the cryptonephric system at 45-hr, the anterior dorsal portion of the rectum projects forward to form the rectal caecum as a result of mitotic divisions.

The number of the epithelial cells of the rectal proper has also been increased apparently. Mitotic figures are most abundant in the epithelium of the third day pupa (Fig. 69). As result of the rapid division, the epithelial cells becomes smaller with large ovoid nuclei located at the basal half of the cell.

Groups of paired large cells are found interrupting the general epithelial cell. These cells will ultimately

form the cortex of the rectal pad. By the time the pupa is 150-hr-old, each developing cortical cell projects a portion of cytoplasm into the lumen (Fig. 70). The paired cortical cells are packed closely so as to form a more or less spherical unit. The cytoplasmic projection of these cells are also ovoid in shape and is separated by the cell membrane along the mid-line of the two cells (Fig. 70). In some cases, this group is composed of three cortical cells (Fig. 71).

With the development of the cortical cells, the radial cells or the cells adjacent to the cortical cells undergo a few alterations. Firstly, these cells elongate and, secondly, they curve against the developing cortical cells so as to cover the basal part of the cells. These cells contain slightly flattened nuclei. The cytoplasm of the developing cortical cells stain deeply with hematoxylin. All these cells are intimately packed and are adhering to the basement membrane closely. At this time, a thin intima is noticeable on the lumen surface of the epiehtlium.

By the 180-hr after pupation, the epithelium other than the developing pad (known as the general epithelium)

is further reduced to a thin layer of cuboidal cells with distinct muscle bands running along its surface. The developing pad unit has grown larger and projected into the lumen distinctly (Fig. 72). The nuclei of the cortical cells flatten and migrate to the centre of the cells. The apical surface of the cells is domed. The lateral radial cells are also flattened and are intimately packed. There are about six to seven layers of these cells on each side, and they surround the cortical cells. The inner layers are actually embedded into the lateral margin of the cortical cells. Junction cells are noticeable in connecting the radial cell and the general epithelium (Fig. 72).

Beneath each of the cortical cell, a space or cavity is formed and is known as the infundibulum. A cluster of very small spherical cells, the medulla, are located between the infundibula just beneath the thin muscularis. The apical surface of the dome of the cortical cells is lined with a thin intima where materials stained darkly with hematoxylin are normally accumulated (Fig. 72).

In a 220-hr-pupa, the nuclei of the developing cortical unit migrate to the apical end of the cells and extend to the lateral margin (Fig. 73; 74, 75). The medulla has increased cell numbers and these occupy the basal portion of the pad. As a result of these alterations, the developing pad is no longer dome-shaped. The cortex is flattened with the nucleus located immediately beneath the apical margin. The cell membrane separating the two cortical cells is no longer evident. Between the nucleus and the lateral lying radial cells, an area of light-staining cytoplasm is normally present. In some cases, the absence of an infundibular space between the cortical cells and the medullary cells is noticeable.

When the rectal pads have fully developed, they persist intact throughout the pupal life. No remarkable alterations are found between the late pupa and the adult. However, in many cases, spaces are found between the apical surface of the cortex and the outerlying intima (Fig. 74).

The general epithelium can be highly condensed. When unfolded, the epithelium is composed of a single layer of cuboidal or squamous cells with dome-shaped apical surface which is lined with a thin intima (Fig. 66).

The epithelial wall of the rectal caecum is said to be identical to that of the general epithelium of the rectal proper (Judy and Gilbert, 1970). Before receiving meconium from the midgut, the epithelial wall of the rectal caecum is highly folded and the epithelial cells are intimately packed together. The cells elongate and are narrow with their nuclei located normally in the apical half of the cell (Fig. 67). This is particularly true in the case of Erionota, in which the rectal caecum will expand 3 fold and project to the anterior abdomen when the rectum is filled with meconium from the midgut. Unidentified vacuoles containing numerous spherical bodies are found located at the luminal end of the cell.

4. Adult

Once the rectal pad has developed in the pre-emergence stage, the structure persists throughout the

remainder of the life of the insect. No further changes are noticeable in the adult.

DISCUSSION

The larva-pupa-adult transformation of the alimentary canal during metamorphosis of Erionota and Euploea is, in general, similar to those of Homaledra sabalella (Gray, 1931) and Hyalophora cecropia (Judy and Gilbert, 1969, 1970). However, in Erionota and Euploea, except in cold winter, no diapause intervenes the pupal stage so that the larva-pupa and pupa-adult transformation is a continuous process.

For the purposes of discussion, the foregut, midgut, and hindgut will be considered separately.

I. FOREGUT:

The foregut of the fifth instar larva is only a straight tube with no diverticulum or protuberance. It is designed to function in the ingestion and temporary storage of food. Apart from the secretion of digestive enzymes by the paired salivary glands and the trituration of food by the paired mandibles, no other physical nor chemical digestion

takes place in the foregut. This agrees with the findings of Lim and Teo (1971) in the digestive enzymes of Agrotis ypsilon, in which no digestive enzymes are normally present in the foregut.

Judy and Gilbert (1970) have suggested that the cuticular spines of the buccal cavity and pharynx in Hyalophora cecropia are designed to grip food particles and direct them posteriorly to the midgut. This function is also obvious in the case of Erionota and Euploea. Moreover, these cuticular spines prevent the regurgitation of ingested food. These spines are sloughed to the lumen together with the intima during metamorphosis. The old intima of the foregut disappeared in a 200-hr-pupa. It is believed (Romoser and Venard, 1967) that the old intima is reabsorbed and resecreted by the epithelial cells to form the new one. However, no cuticular spines are found on the new intima. This indicates that the spines are no longer needed in the nectar-feeding adult.

The larval crop apparently serves as a reservoir to store the ingested food temporarily. This enables the larva to feed continuously. Observation on the ingested food clippings and the faecal pellets in the hindgut reveals

that the larva is able to digest only 1/3 to 1/2 of the ingested food.

The larval oesophageal invagination is unlikely suited the function of preventing regurgitation of food from the midgut to the foregut. Instead, it serves to ensure food entering the peritrophic membrane, so as to protect the midgut from abrasion as suggested by Wigglesworth (1972).

The reduction of the diameter of the foregut during metamorphosis is probably an adaptation to the alteration of the mode of feeding. The mouthparts of the insect have changed completely from the chewing type of the larva to the sucking type of the adult. The narrow foregut forms a continuous capillary of the siphon, so that the sucking up of liquids is much easier with the help of capillarity.

During the progress of adult development, the posterior foregut undergoes a series of alterations although the anterior foregut remains reduced. The major alterations are the development of the adult crop, the proventriculus and the adult oesophageal invagination. These adult organs

are derived from the posterior part of the foregut -- the anterior imaginal ring.

As Kathuria (1972) have said: "The findings on the metamorphosis of the foregut in insects are contradictory". Deegener (1908) in Malacosoma castransis, Bordas (1911) in various Lepidopterous larvae and Hufnagel (1918) identified the region intervening the oesophageal invagination and the midgut as a regenerative region. Perez (1910) in Calliphora, recognized the presence of this region and showed that the adult crop is derived here. He, however, doubted whether this region played any part in the metamorphosis of Lepidoptera. Gray (1931) in Homaledra termed this region as the "histoblastic disc" and claimed that the larval foregut degenerates during metamorphosis and is replaced by the proliferation of this disc. Henson (1931) in Vanessa urticae stated that the anterior imaginal ring plays so little in the metamorphosis. However, in 1946, he revised his earlier opinion and said that "the behaviour of the ring at metamorphosis is most diverse".

Romoser and Venard (1967) in Aedes triseriatus, Bahadur and Kathuria (1971) and Kathuria (1972), in Papilio aristolochiae, showed that the three adult organs are

derived from the second region of the oesophageal invagination. Although region 4 and region 5 develop to form two dorsal diverticula in Aedes triseriatus (Romoser and Venard, 1967), no such diverticula are noticeable in Lepidoptera. Moreover, region 4 and region 5 will ultimately degenerate. This is also true in Erionota and Euploea in which no degeneration of the foregut occurs except region 4 and region 5 of the oesophageal invagination. Verson (1905) in Bombyx mori, and Deegener (1908) in Malocosoma, have arrived the same conclusion stating that no replacement of cells are noticeable in the foregut during metamorphosis but condensation and rearrangement of cells.

The function of the adult crop is obscure since the crop is fully filled with air. However, the function if the crop is apparently not digestive. It has been suggested that the inflation of air to the crop is an assistance in insect moulting or adult ecdysis in Lepidoptera (Stober 1927, Wigglesworth 1972). Judy and Gilbert (1969), in Hyalophora cecropia, believed that the crop provides a compensatory mechanism for maintaining haemocoel volume during the wing expansion shortly after adult ecdysis. These findings, however, are contradictory.

In the present study, specimens of various stages after adult ecdysis were dissected to see the relationship between the inflation of the crop and expansion of wings. These dissections show that the crop of an adult immeiately after ecdysis is uninflated. In a 20-min-adult, the crop is 1/3 to 1/2 inflated whilst the wings are half way expanded. As expected, the wings of the adult, at about 40 minutes after emergence, are fully expanded and the crop is now fully inflated. Dissections of old adults repeatedly show the crop is fully expanded, but the air volume varies from one another.

Conclusively, this finding supports Judy and Gilbert's (1969) proposed function for the crop which is a compensatory mechanism for maintaining haemocoel volume during the expansion of the wings. In addition, the inflated crop may provide an assistance, similar to the gut of adult mayfly, for aerostatic purposes (Pickles, 1931; Grandi, 1950) since the air volume found in flying adults varies from one another.

The proventriculus is a small tube which intervenes between the adult crop, the anterior foregut and the midgut. It is surrounded by a thick mass of

muscules and fats during adult development. The proventriculus serves as a true cardiac sphincter to regulate the passage of food materials to the midgut as Snodgrass (1935) suggested. If the proposed additional function for the adult crop is correct, then the proventriculus may function like the epiglottis of mammals. Presumably, during the inhalation of air, the proventriculus contracts and occludes the lumen that leads to the midgut. In other words, the function of the proventriculus is to prevent the entry of air to the midgut.

Most of the adults of Lepidoptera are nectar feeders. In many cases, such as Hyalophora cecropia (Judy and Gilbert, 1969) and Eriogyna pyretorum (Fung, unpublished observation), adults never feed at all. The function of the oesophageal invagination is, therefore, clearly not as that of the larva. Perhaps the major function of the adult oesophageal invagination is, similar to that of the proventriculus, to prevent the entry of air to the midgut.

II. MIDGUT:

The midgut is generally regarded as the digestive and absorptive chamber of the entire alimentary canal. It

has been shown by Cheung (1966) that, in the larvae of rice stem borers, the anterior and middle portions of the midgut mainly deal with enzymatic hydrolysis of foodstuffs, and the posterior zone absorbs the digested food. However, the functional differentiation of the midgut is not immediately obvious by observing the histology only.

The epithelial wall is made up of 2 types of tall cells and the wedge-like regenerative cells. The tall cells are believed to be responsible for digestion and absorption. Vesicles are normally found within the space between the epithelium and the peritrophic membrane. The question remains unanswered is that whether these vesicles are secretory products or degenerative cytoplasm extruded from the epithelium. However, the number of these vesicles becomes increased when the larva reaches the prepupal stage.

The midgut epithelium undergoes the most drastic changes of the gut during metamorphosis. The tall cells of the larval epithelium are completely replaced by the larval regenerative cells which develop to form the columnar epithelium of the pupa. Judy and Gilbert (1970) regarded the pupal midgut as no longer a digestive organ but serves as a storage organ for the yellow body. However,

the function of the pupal and adult midgut, at least in Erionota and Euploea, is apparently digestive. The yellow body in the pupal midgut is broken down gradually and presumably absorbed and reused by the pupa for reconstruction. The remnants of the yellow body is discharged to the hindgut after the completion of the reorganization of the hindgut and is later egested after emergence.

The adult midgut is also digestive. However, the midgut is composed of columnar cells and adult regenerative cells. No goblet cells are noticeable. In the newly emerged adult of Euploea, the nuclei of the epithelial cells are located in the basal halves of the cells. In an old adult, the nucleus tends to migrate to the luminal half of the cell and, at more or less the same time, the columnar cell has become club-shaped. In Erionota, although the columnar cells have altered to club-shaped, the nuclei remain located in the basal halves of the cells.

The peritophic membrane is an universal structure for all Lepidopterous larvae (Wigglesworth, 1972). The membrane is no doubt functioning in protecting the midgut epithelium from abrasion by hard fragments in the food. The membrane found enveloping all the food contents of the

midgut is obviously of delamination type (Waterhouse, 1953; Smith, 1968; Wigglesworth, 1972; Richards and Richards, 1977). The presence of peritrophic membrane in the larval midgut is undoubtedly an adaptation.

The peritrophic membrane is not an universal structure for all Lepidopterous adults. In Erionota, no peritrophic membrane has been found in any adult specimen. In contrast to this, a thin tubular peritrophic membrane is found running from the region between the oesophageal invagination and the anterior end of the midgut to the posterior midgut of a newly emerged adult of Euploea. In an old adult, the membrane is produced by a ring of cells at the anterior end of the midgut as suggested by Waterhouse (1953), Wigglesworth (1972), and Richards and Richards (1977). However, the function of the peritrophic membrane in the adult is obscure. It is curious to find that no peritrophic membrane is present in the adult Erionota. This is supported by the works of Waterhouse (1953). He suggested that adult butterflies of Hesperiidae have lost their peritrophic membrane during evolution.

III. HINDGUT:

Situated immediately posterior to the midgut is

the posterior imaginal ring which is composed of small cuboidal cells. However, unlike the anterior imaginal ring, this ring plays very little part during metamorphosis. No distinct structures are formed from this ring. The epithelial protuberance is a structure corresponding to the oesophageal invagination of the foregut. On the posterior half of this protuberance, spicular intima are produced. Cuticular spines are also found at the posterior part of the pyloric valve and are arranged in rows. It is difficult to suggest any function for these curious structures. Owing to their tiny size and the presence of sphincter, it seems most unlikely that they prevent regurgitation from the ileum nor grip food and direct them posteriorly. Hypothetically, these spines and the protuberance are vestigitial structures which lost their function in the progress of evolution.

During the pupal stage, "tissue plugs" are found located at the entry as well as the exit of the midgut. Gray (1931) recognized the presence of this structure in the pupa of Homatedra and called it "tissue plug". However, no proposed function has been given. Actually, it is a cluster of cells which appear a few days after pupation

and disappear before emergence. Because of their small size and their weak appearance, these tissue plugs, although situated at both margins of the midgut like valves, have no known function. Besides, the entry and exit of the midgut during most of the time of the pupal stage have already sealed by the old intima sloughed off from the foregut and hindgut respectively.

The pyloric valve and the rectal valve are very muscular. They are well adapted to serve as sphincters which seal the ileum as a closed chamber for the formation of faeces as suggested by Reinecke et al., (1973) in Manduca sexta.

In some other Lepidopterous larvae, such as in Heliothis (Chauthani and Callahan, 1967; Chi et al., 1975), protuberances are found in the hindgut, but in the larvae of Erionota and Euploea, no protuberance or diverticulum is noticeable. Drecktrah et al., (1966) have reported that the middle portion of the hindgut of Ostrinia nubilalis is only an undifferentiated tube. On the other hand, such portion in the hindgut of Hyalophora cecropia (Judy and Gilbert, 1969) and Manduca sexta (Reinecke et al., 1973) is well differentiated into the distinct ileum and colon.

In Erionota and Euploea, however, the demarcation of the ileum and colon is obscure and the epithelium is undifferentiated.

It is almost universal among Lepidopterous larvae, with the exception of "aquatic larvae" such as Chilo (Cheung, 1966), that the terminal portion of the Malpighian tubules are intimately applied to the wall of the rectum forming the cryptonephridial system (Saini, 1964). The cryptonephridial system of Erionota and Euploea agrees with the descriptions of Henson (1937), Drecktrah et al., (1966), Judy and Gilbert (1969), and Reinecke et al., (1973). According to the statement of Saini (1964) for other Lepidoptera, the larvae of Erionota and Euploea can be classified as "green feeding form". Chauthani and Callahan (1967) have reported that rectal pads are present in Heliothis larvae, but in the larva of Erionota and Euploea, they are absent from the hindgut. Wigglesworth (1972) and Ramsay (1976) have suggested that the cryptonephridial system of the rectum plays an important part in the process of water reabsorption.

Similar to the foregut, the pupal and adult hindgut plays an important role in adult physiology. During adult development, a series of drastic changes are noticeable in

the hindgut. These include the development of the long, folded, unspecified ileum; the association of the Malpighian tubules to the ileum; the degeneration of the larval rectal complex and the formation of the adult rectal pouch as well as the rectal pads.

During the early stage of pupal development, large quantity of wastes are produced as a result of degeneration of various tissues. Wastes are collected by the Malpighian tubules and are later discharged into the hindgut. It is obvious that water recirculation through the cryptonephridial system is most necessary especially when the pupa has to withstand dessiccation. The reabsorption of water is believed to be carried out by the rectal glands or rectal pads (Wigglesworth, 1932, 1972).

Judy and Gilbert (1970) reported that the structure of the rectal pads of the adults of Antheraea polyphenus, Samia cynthis, and Hyalophora cecropia (all are Saturniidae and do not feed) are identical to that of the nectar-feeding adult of Manduca sexta of Sphingidae. Moreover, the structure of the rectal pads of Erionota and Euploea are essentially the same as those mentioned. However, it is not surprising to find that the rectal pads are identical in fluid feeding

species and those that do not feed at all. The rectal pads in both types of adults are functional.

In the fasting imago, the reabsorption of water is most necessary in order to maintain water conservation in the body, since there is no further water intake. On the other hand, in the fluid feeder, although water supply is presumably adequate, relatively high quantity of metabolic wastes is produced at the same time; the need of water conservation may still be necessary.

In addition, the Malpighian tubules are in some cases adhered to the ileum intimately; this may be considered as that water can be reabsorbed through the ileal wall to the Malpighian tubules before reaching the rectal pads.

It is interesting to find that the ileal wall of Erionota is rather smoother than that of Euploea, which is highly folded. Moreover, the Malpighian tubules of the former attach to the ileal walls loosely while that of the later intimately adhere to the ileal wall in a ziz-zag manner. These differences are most unlikely individual variations but seemingly an adaptation to the flying behaviour of the adult.

Euploea is a typical representative of Danainae (Family Nymphalidae). It is a sun-lover, flying and gliding around flowers and trees all day long. In contrast, Erionota, although a swift flyer, spent most of the time resting on the underside of banana leaf. It flies, when being disturbed, only for short distances around banana cultivation. It is obvious that Euploea is more active than Erionota; and that the quantity of metabolic wastes is comparatively higher. The need of water for excretion is most necessary and the highly folded ileal wall and the closely associated Malpighian tubules may be designed to meet the need.

When the pupa reaches the pre-emergence stage, the midgut empties its contents to the hindgut. The rectum will then serve as a storage chamber temporarily for the accumulation of excreta.

Key for abbreviations used in Fig. 8 to Fig. 75

A	:	anterior region of the imaginal ring
amg	:	anterior midgut
ai	:	anterior imaginal ring
c	:	columnar cell
cc	:	central cavity
cd	:	common Malpighian ampulla exit duct
ce	:	cryptonephric epithelium of the rectal sac
ci	:	cuticular intima
cm	:	circular muscle
cms	:	circular muscle sheet
cn	:	nucleus of columnar cell
cp	:	cytoplasmic projection
cr	:	crop
csm	:	circular sphincter muscle bands
ct	:	cortical cells
dcr	:	developing adult crop
di	:	detached intima of rectal sac
dm	:	dilator muscle
e	:	epithelium
f	:	faeces
fb	:	fat body

fd : food

fg : foregut

g : goblet cells

gb : gobular body

ge : general epithelium

gn : nucleus of goblet cell

hg : hindgut

if : infundibulum

il : ileum

ip : inner perinephric membrane

is : inner perinephric space

it : inner tubules of the rectal sac

j : junction cells

lm : longitudinal muscle

lp : larval pylorus

lu : lumen

m : muscle

mc : medulla cell

mf : mitotic figure

mg : midgut

ms : medial space

mt : Malpighian tubules

n : nucleus

ne : normal epithelium

oe : oesophagus

oi : oesophageal invagination

op : outer perinephric membrane

os : outer perinephric space

ot : outer tubules

P : posterior region of the imaginal ring

pc : pyloric cone

ph : pharynx

pi : posterior imaginal ring

pm : peritrophic membrane

pmg : posterior midgut

pr : pupal regenerative cells

ps : perinephric space

pt : protuberance of the pyloric cone

pv : proventriculus

R1-R5 : The five regions of the oesophageal invagination

ra : radial cell

rc : rectal caecum

rd : rectal duct

re : rectum

rf : reflection of the anterior region over posterior region of imaginal ring

rg : regenerative cell

rp : rectal pad

rs : rectal sac

rv : rectal valve

s : spines

sb : striated border

sm : sphincter muscle

smi : smooth intima

sph : spherules

spi : spiculated intima

spr : spiculated intima ring cell

sr : sclerotized ring

ss : subcuticular space

t : trachea

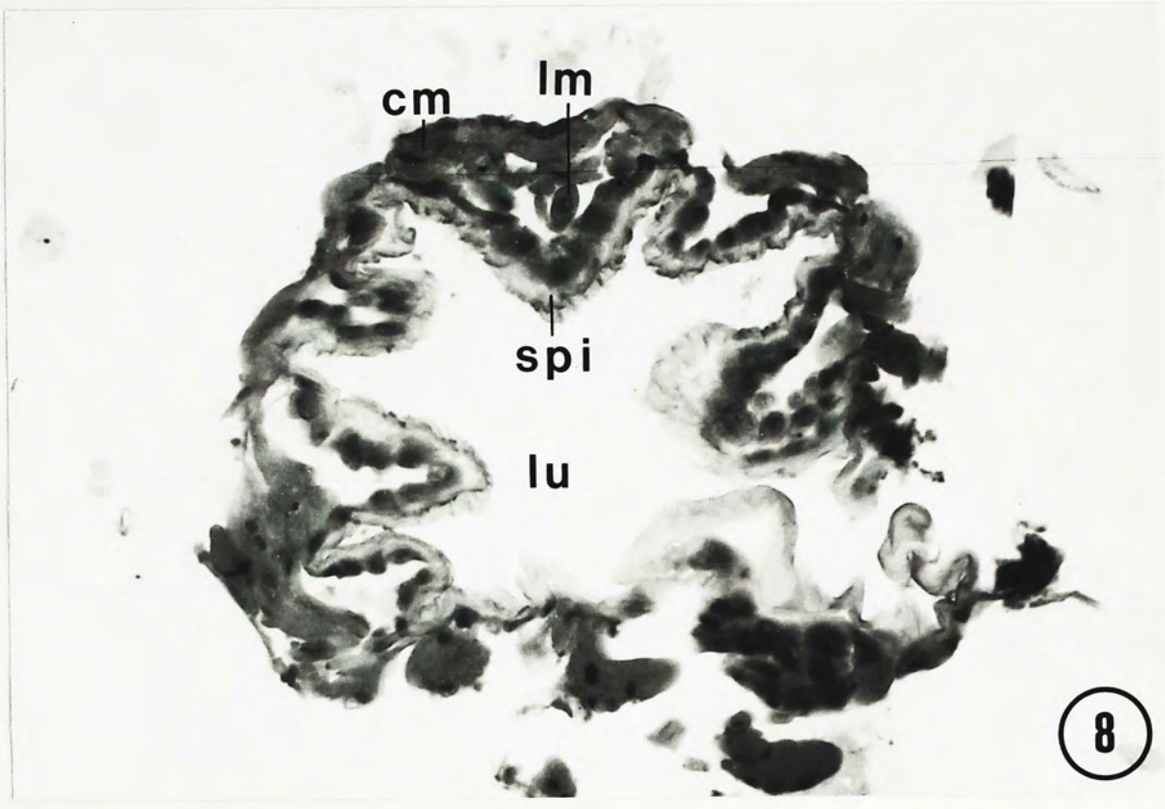
tp : tissue plug

ve : vesicles - nucleated or non-nucleated cytoplasm extruded from the epithelial cells

yb : yellow body

Fig. 8 Transverse section of the pharynx of an active feeding 5th instar larva (Euploea). Note the folded, spiculated epithelium and the strong circular muscle bands (200x).

Fig. 9 Transverse section of the anterior oesophagus of the 5th instar larva of Euploes. Note the thick intima and the highly folded epithelium (200x).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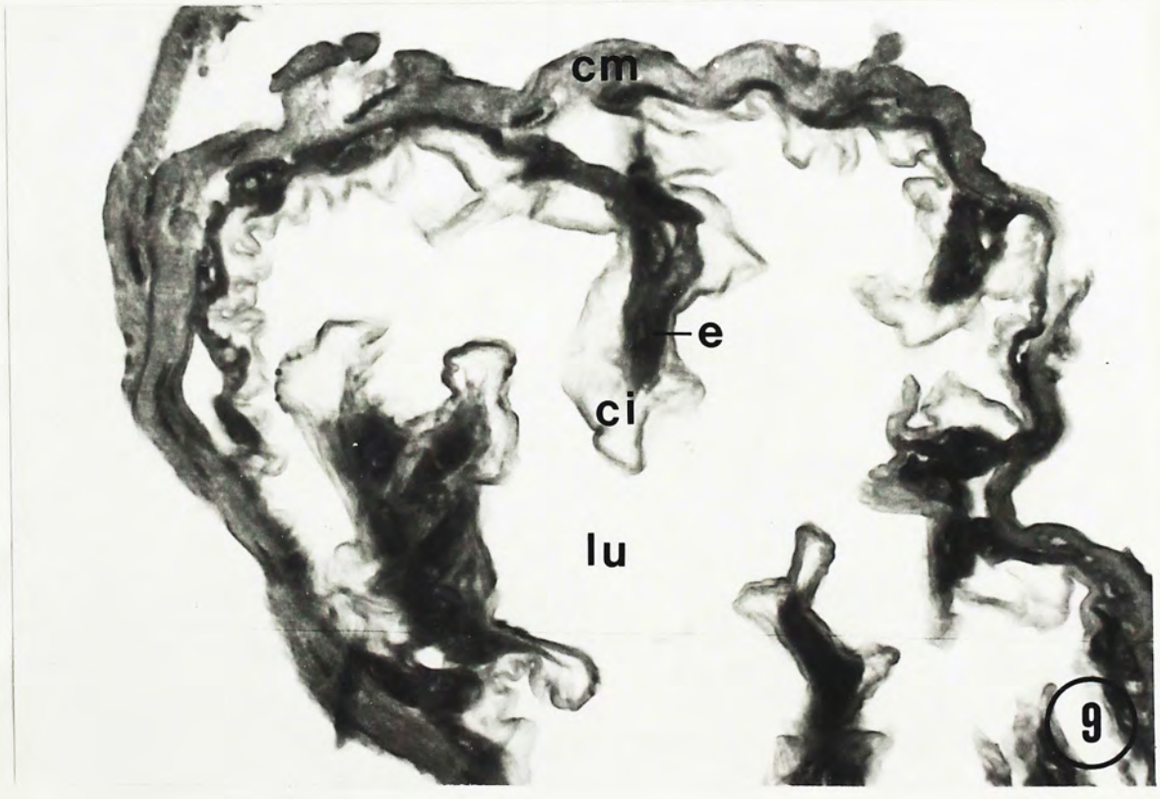
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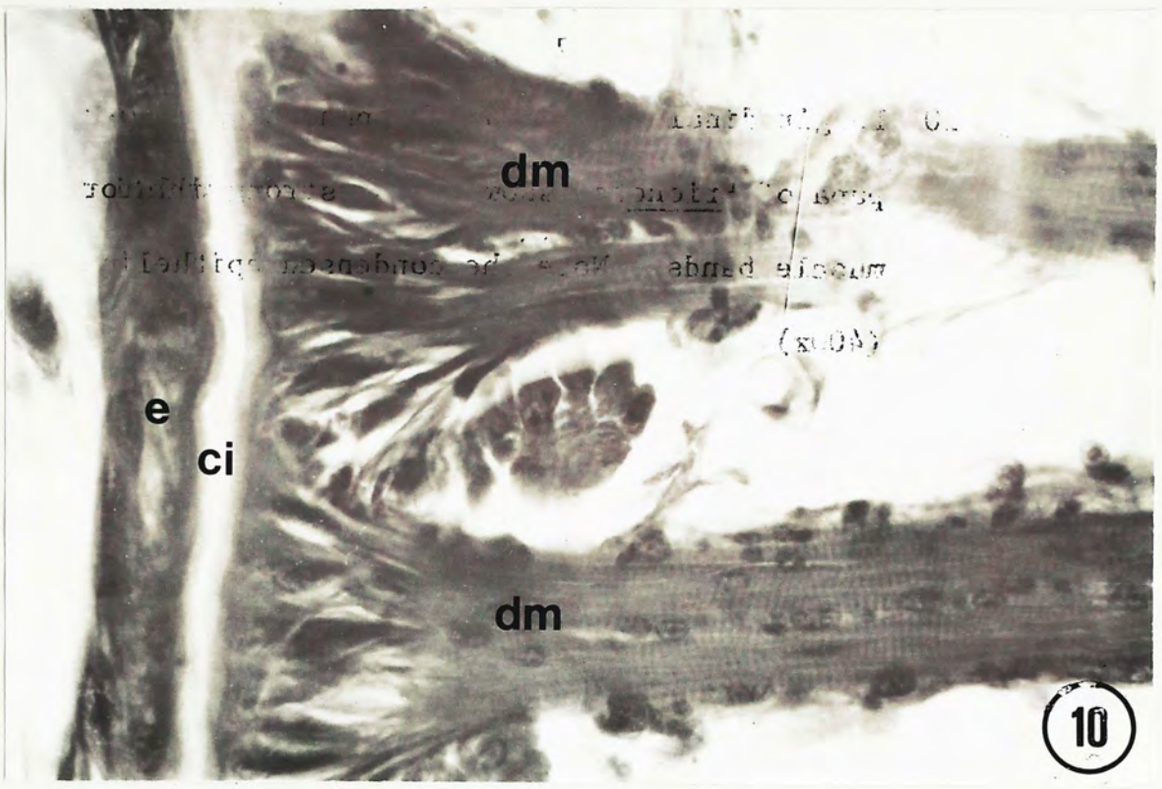
Fig. 10 Longitudinal section of the pharynx of a 0-hr-pupa of Erionota, showing the strong dilator muscle bands. Note the condensed epithelium (400x).

Fig. 11 Transverse section of the oesophagus of a 24-hr-pupa of Euploea, showing the condensation of the epithelium. Note the epithelium is highly folded (400x).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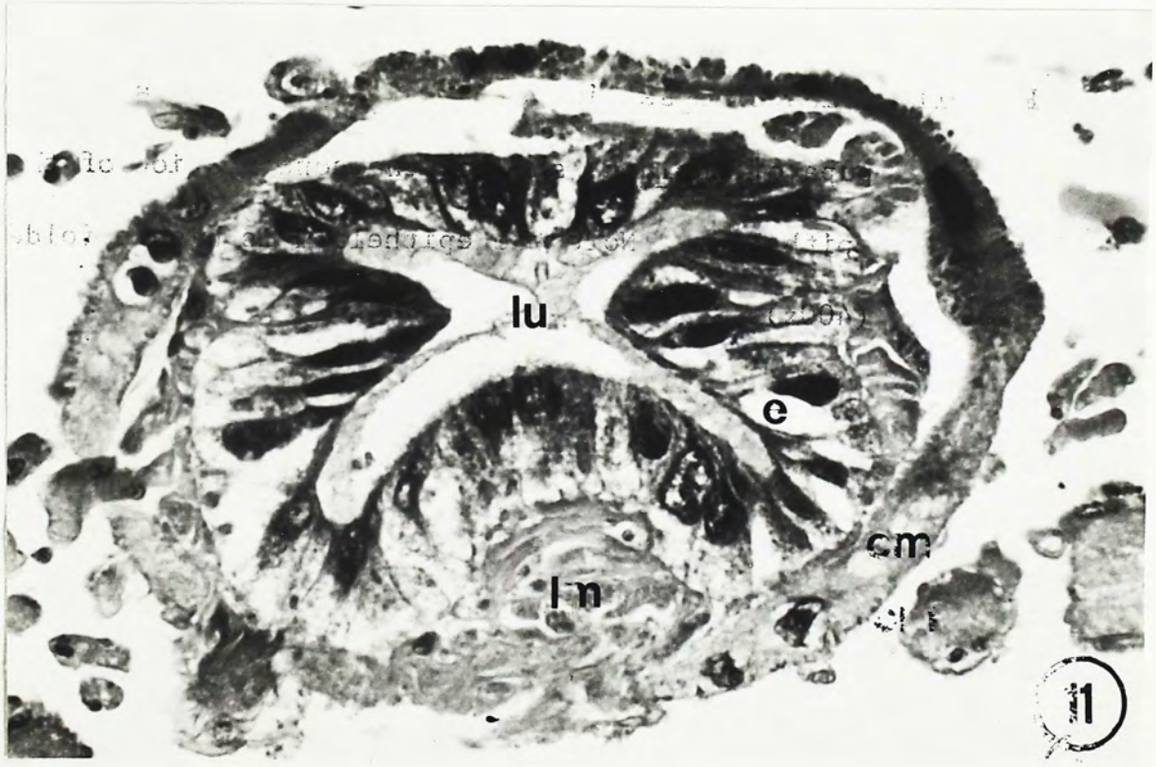
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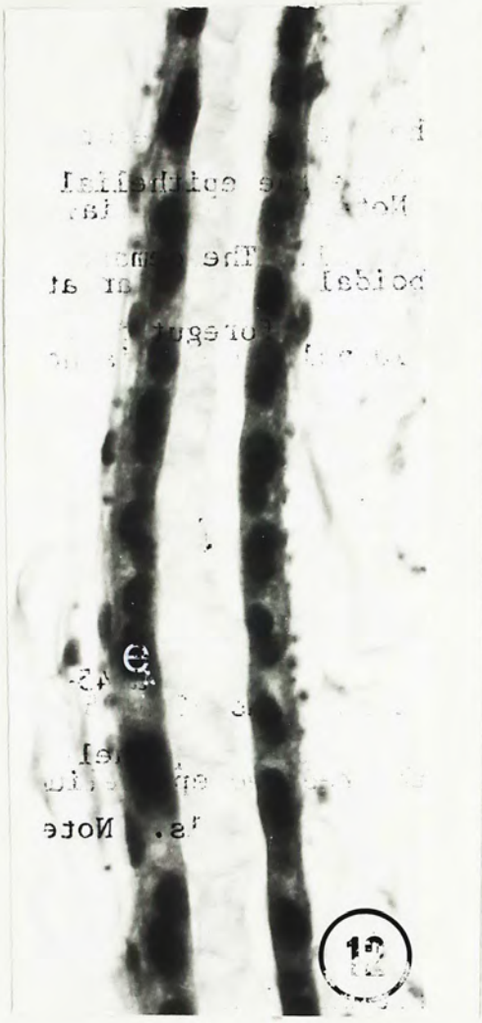
Fig. 12 Longitudinal section of the anterior foregut of a 35-hr-pupa (Erionota). Note the epithelial cells are more or less cuboidal. The demarcation of various regions of the larval foregut is no longer obvious (200x).

Fig. 13 Transverse section of the oesophagus of a 45-hr-pupa (Erionota), showing the reduced epithelium which is now composed of cuboidal cells. Note the darkly staining globular bodies (arrowed) which indicate the degeneration of the outer-lying muscles (400x).

Fig. 14 Transverse section of the anterior foregut of a 150-hr-pupa (Erionota), showing the epithelium and the old intima. Note the epithelium is composed of squamous cells. The epithelium persists this structure throughout the remainder of the insect's life (400x).



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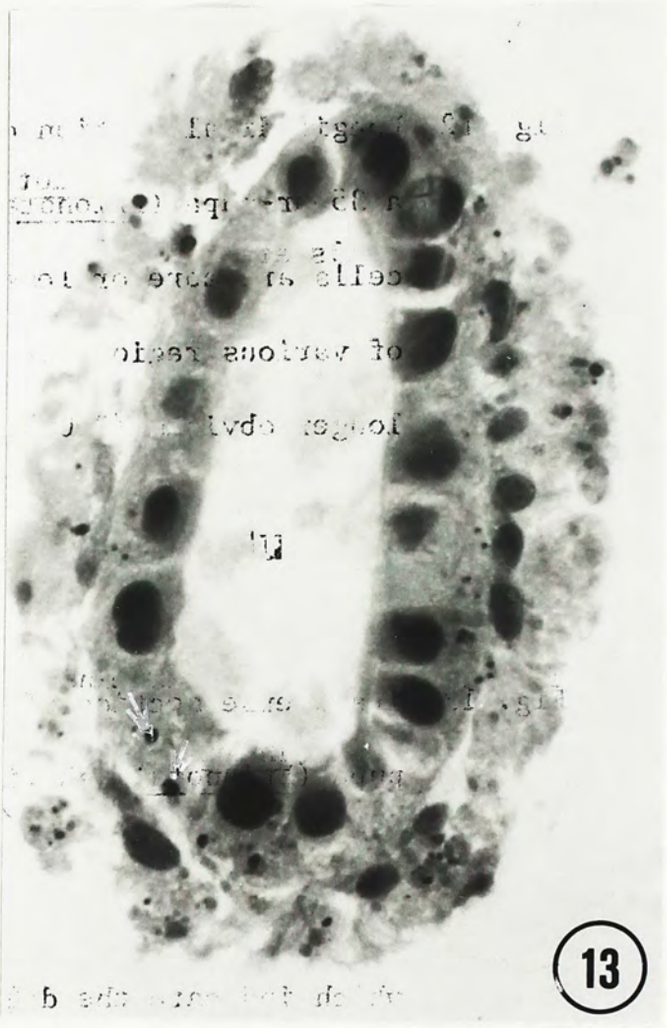

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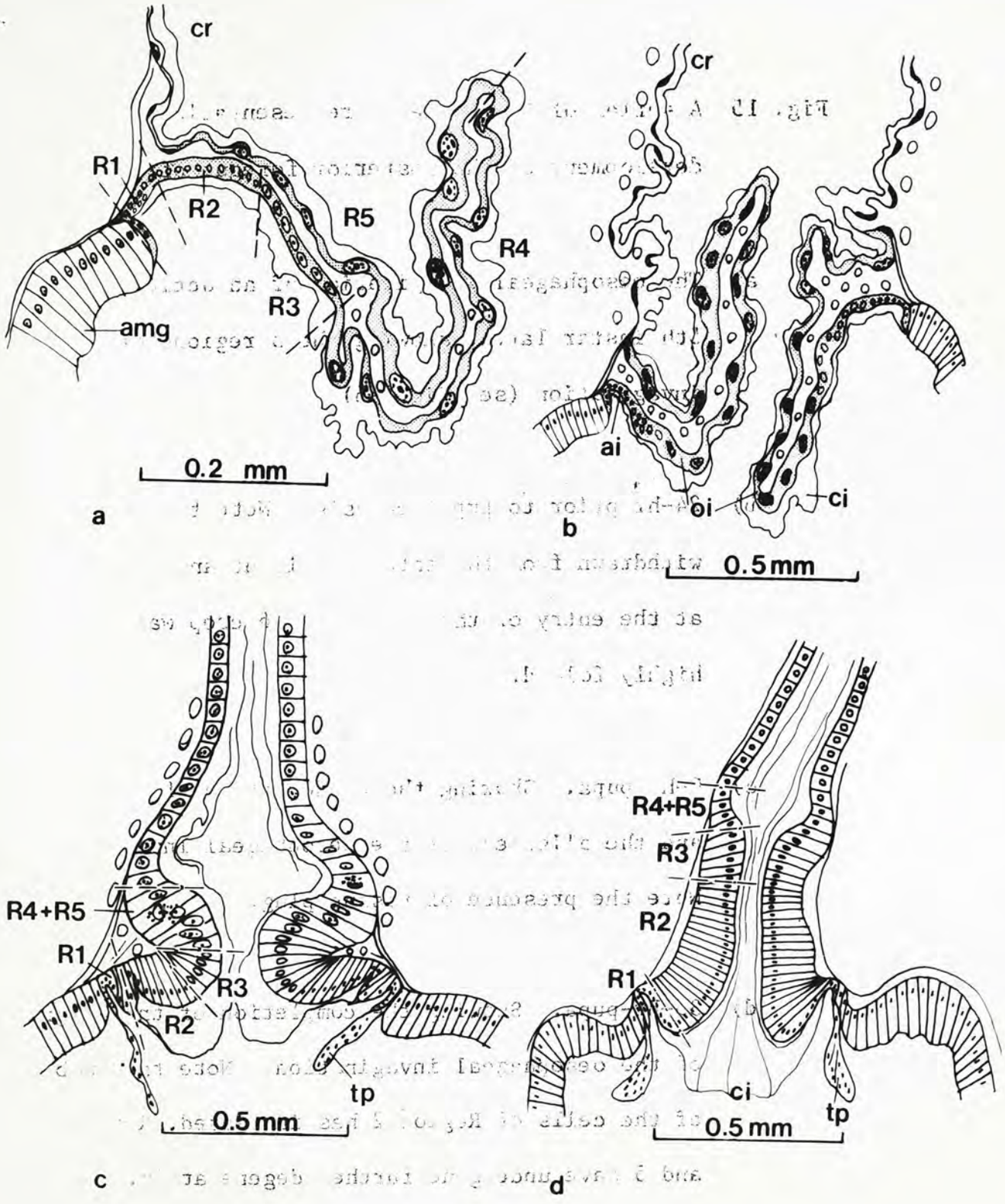
Fig. 15 A series of diagrammatic representations of the development of the posterior foregut of Erionota.

a) The oesophageal invagination of an active feeding 5th instar larva, showing the 5 regions of the invagination (see Fig. 16).

b) 24-hr prior to pupal ecdysis. Note the valves are withdrawn from the anterior midgut and are situated at the entry of the midgut. The crop walls are highly folded.

c) 0-hr-pupa. Showing the condensation of the foregut and the alignment of the oesophageal invagination. Note the presence of tissue plug.

d) 35-hr-pupa. Showing the completion of the alignment of the oesophageal invagination. Note the number of the cells of Region 2 has increased; Region 4 and 5 have undergone further degeneration.

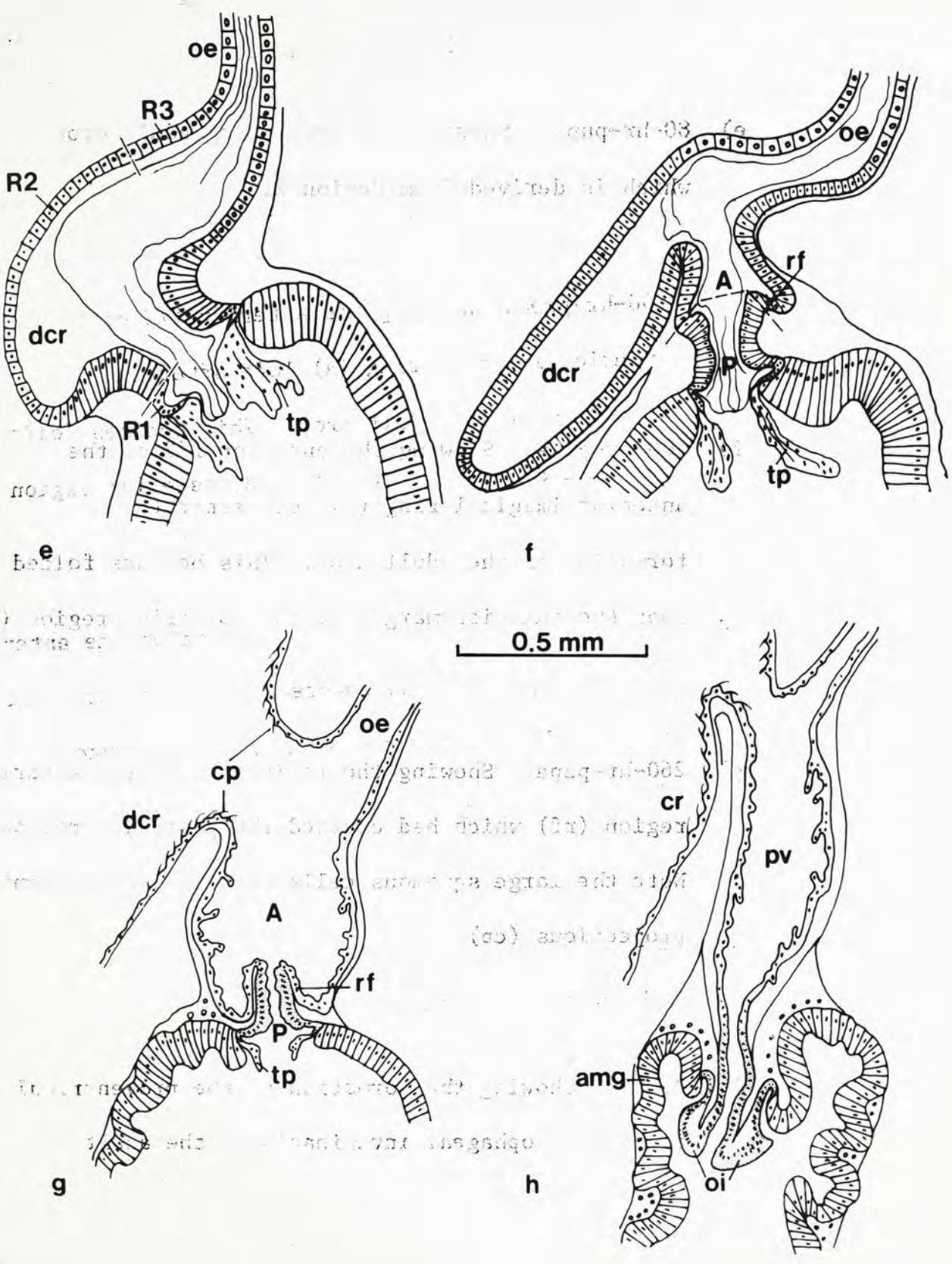

cr
R1
R2
R5
R4
R3
amg
0.2 mm
a
cr
ai
oi
ci
0.5mm
b
R4+R5
R1
R3
R2
tp
0.5 mm
c
R4+R5
R3
R2
R1
ci
tp
0.5 mm
d

e) 80-hr-pupa. Showing the developing adult crop which is derived from Region 2.

f) 100-hr-pupa. Showing the anterior 1/2 of the anterior imaginal ring (A) left after the formation of the adult crop. This becomes folded upon the anterior margin of the posterior region (P).

g) 260-hr-pupa. Showing the reflection of the anterior region (rf) which had covered the posterior region(P). Note the large squamous cells with long cytoplasmic projections (cp).

h) Adult. Showing the formation of the proventriculus and the oesophageal invagination of the adult.


oe
R3
R2
dcr
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tp
e
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A
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0.5 mm
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Fig. 16 Longitudinal section of the larval oesophageal invagination at 48 hours prior to pupal ecdysis (Erionota). Note Region 1 to Region 5 and their thick intima (80x).

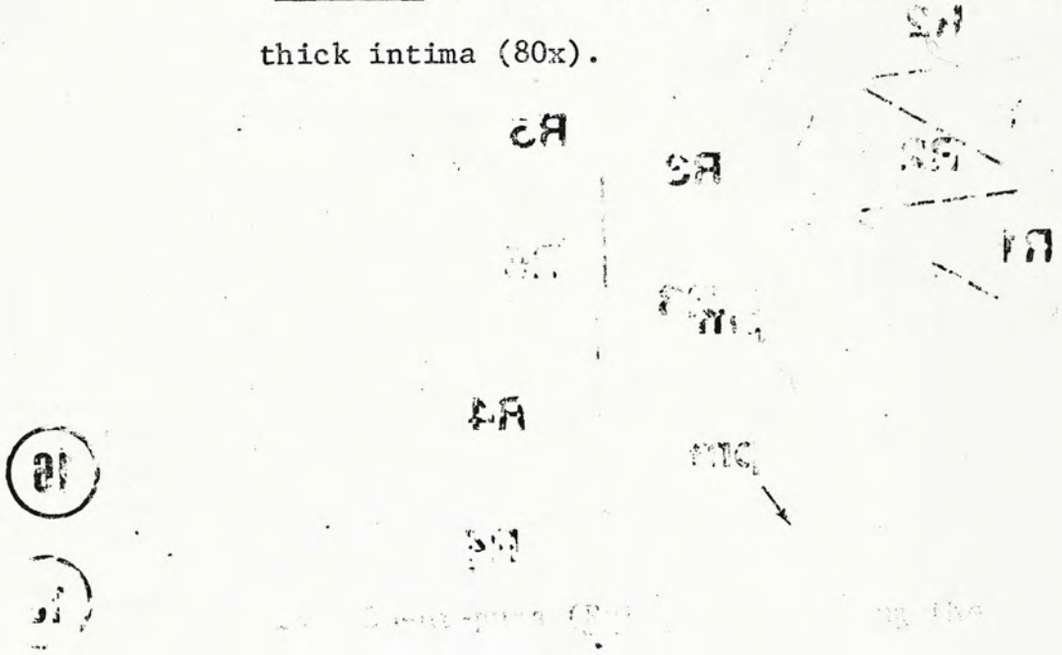
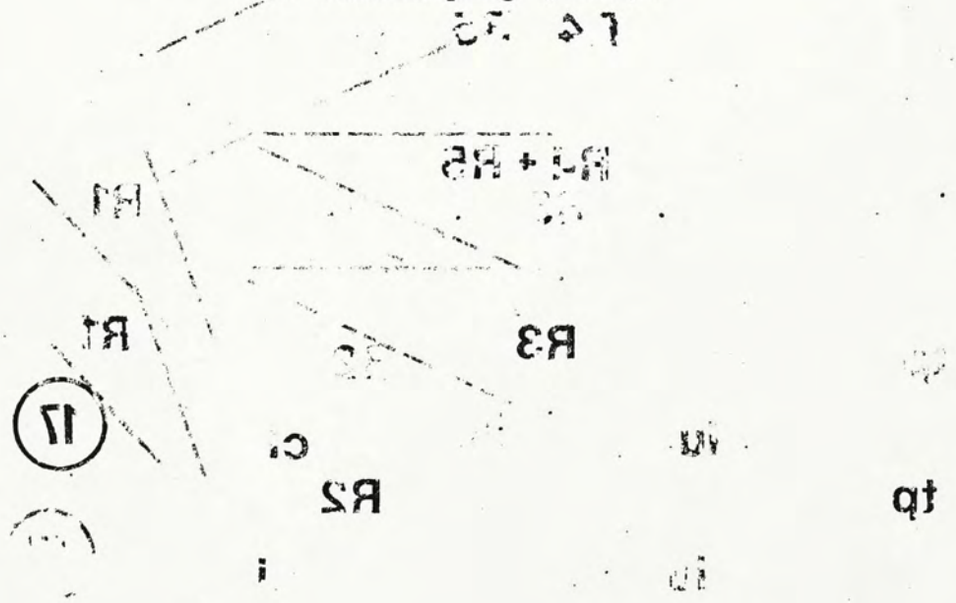
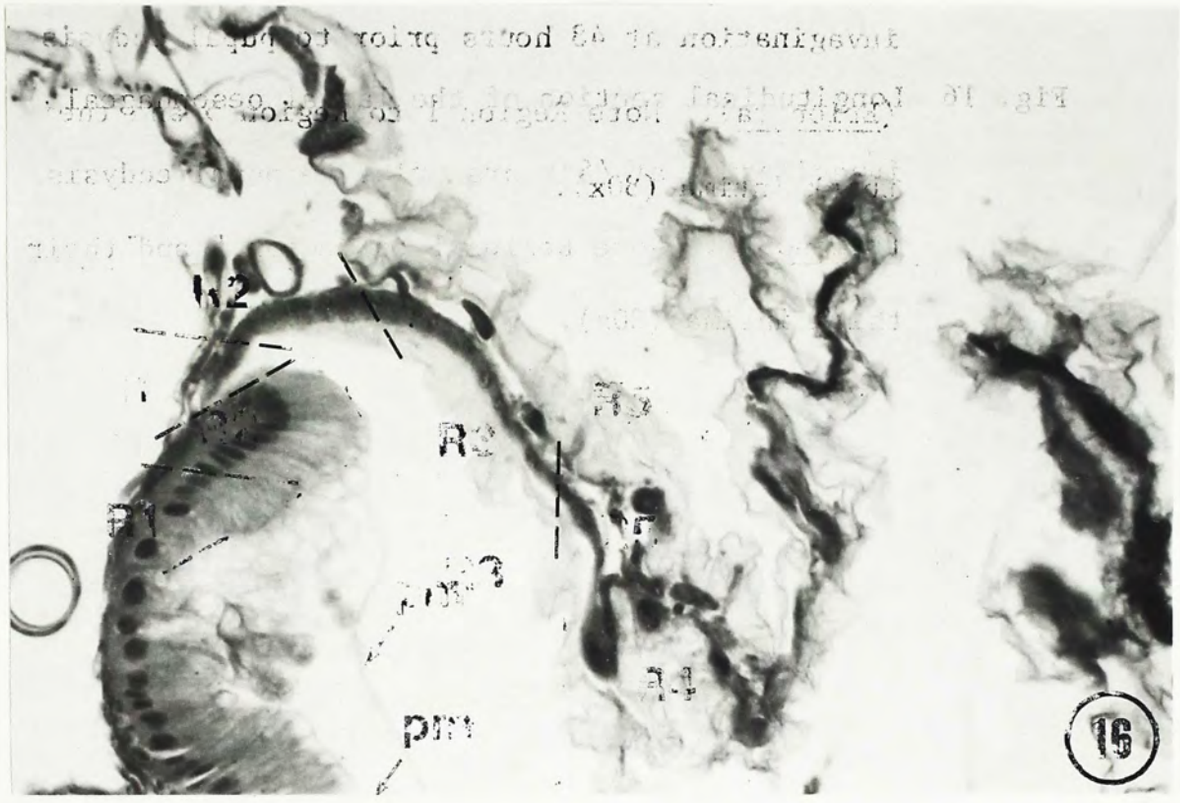


Fig. 17 Longitudinal section of the oesophageal invagination in a 35-hr-pupa (Erionota), showing the condensation of the oesophageal invagination. Note the presence of tissue plug (200x).

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pm
16

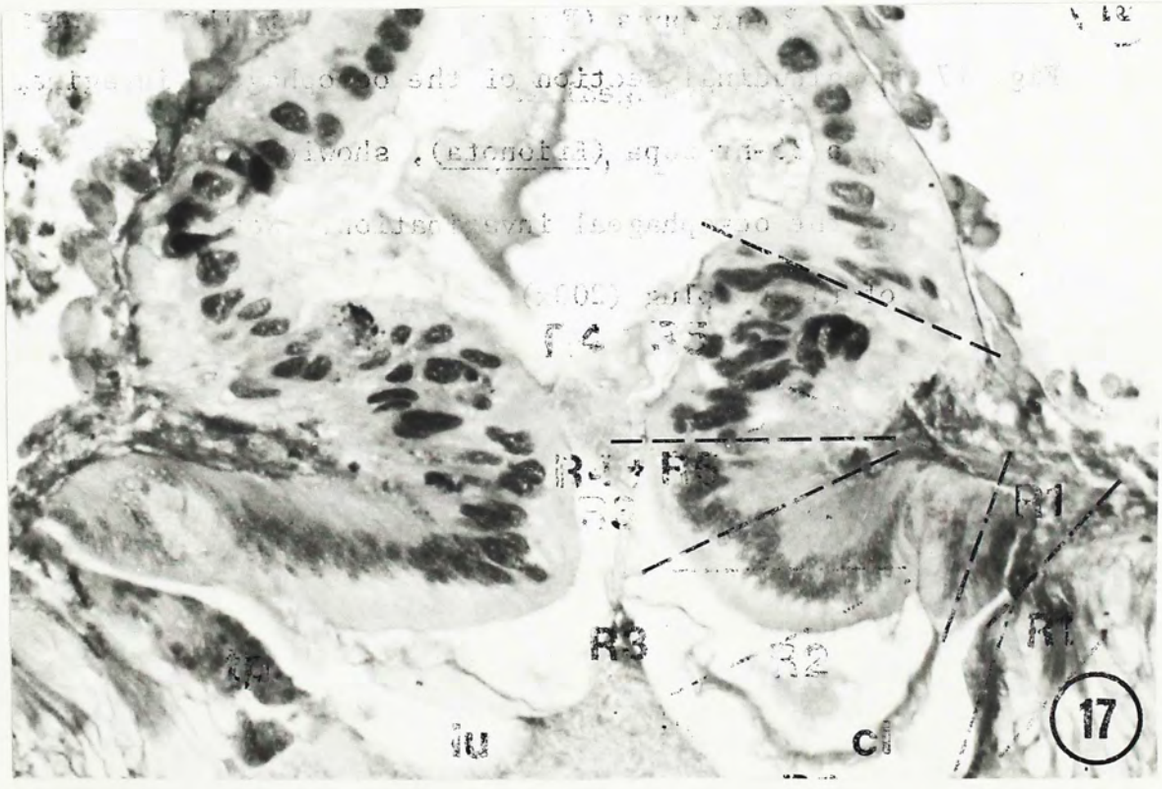
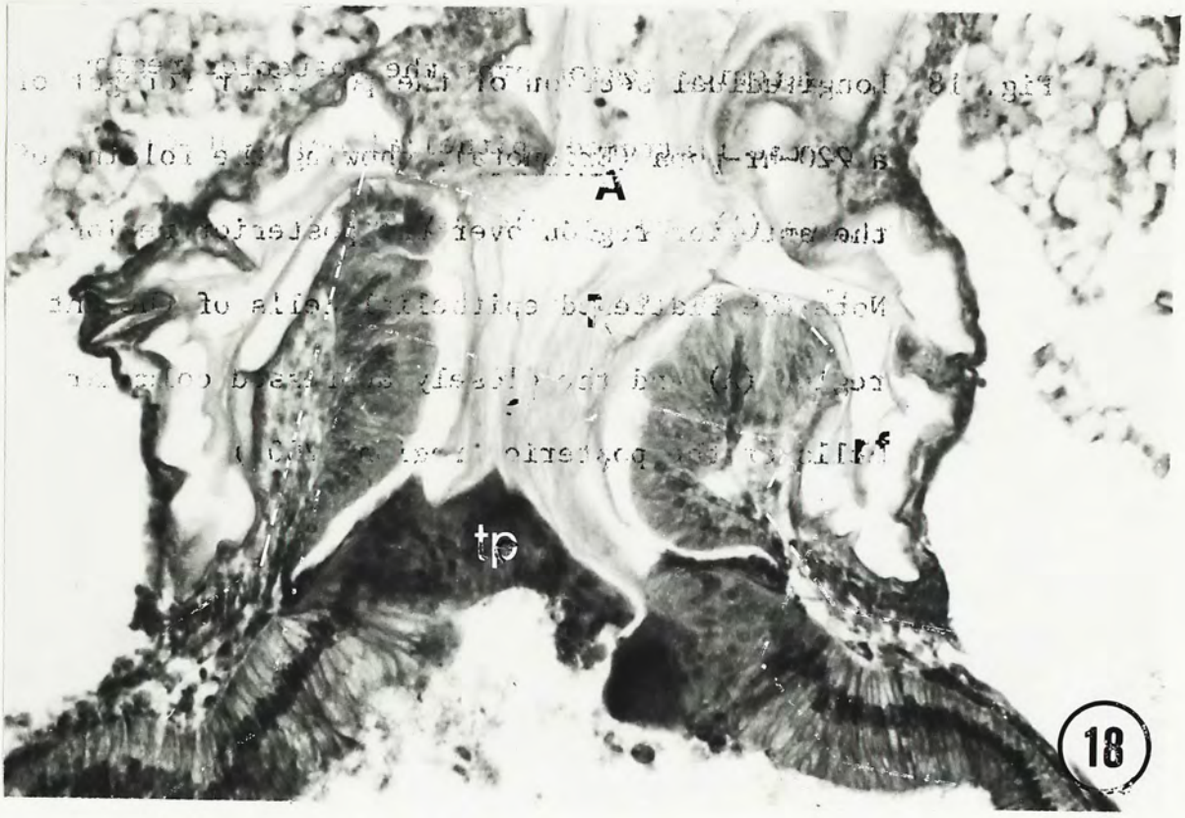

R1
R3
R2
ul
cl
17

Fig. 18 Longitudinal section of the posterior foregut of a 220-hr-pupa (Erionota), showing the folding of the anterior region over the posterior region. Note the flattened epithelial cells of the anterior region (A) and the closely appressed columnar cells of the posterior region (200x).

Fig. 19 Longitudinal section of the posterior foregut of the adult of Erionota, showing the proventriculus and the adult oesophageal invagination. Note the adult oesophageal invagination is formed by folding the double-layered wall of the posterior region posteriorly into the midgut (80x).



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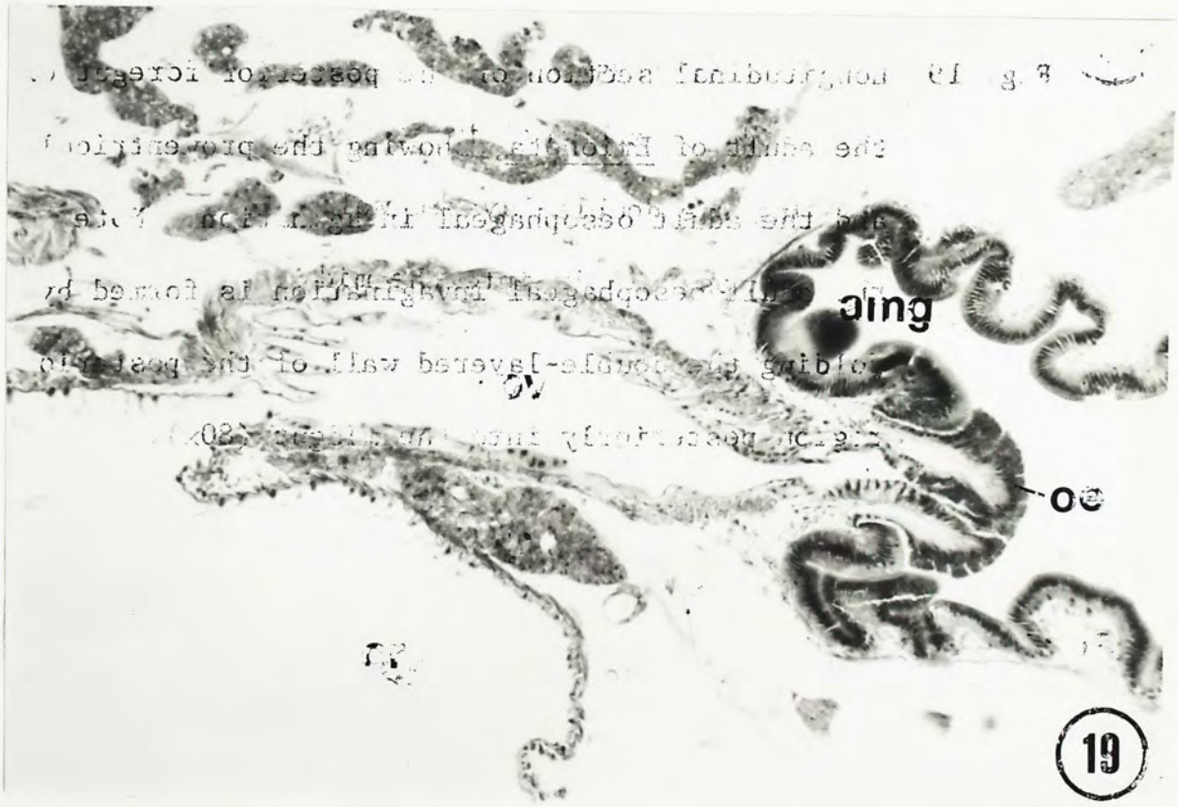

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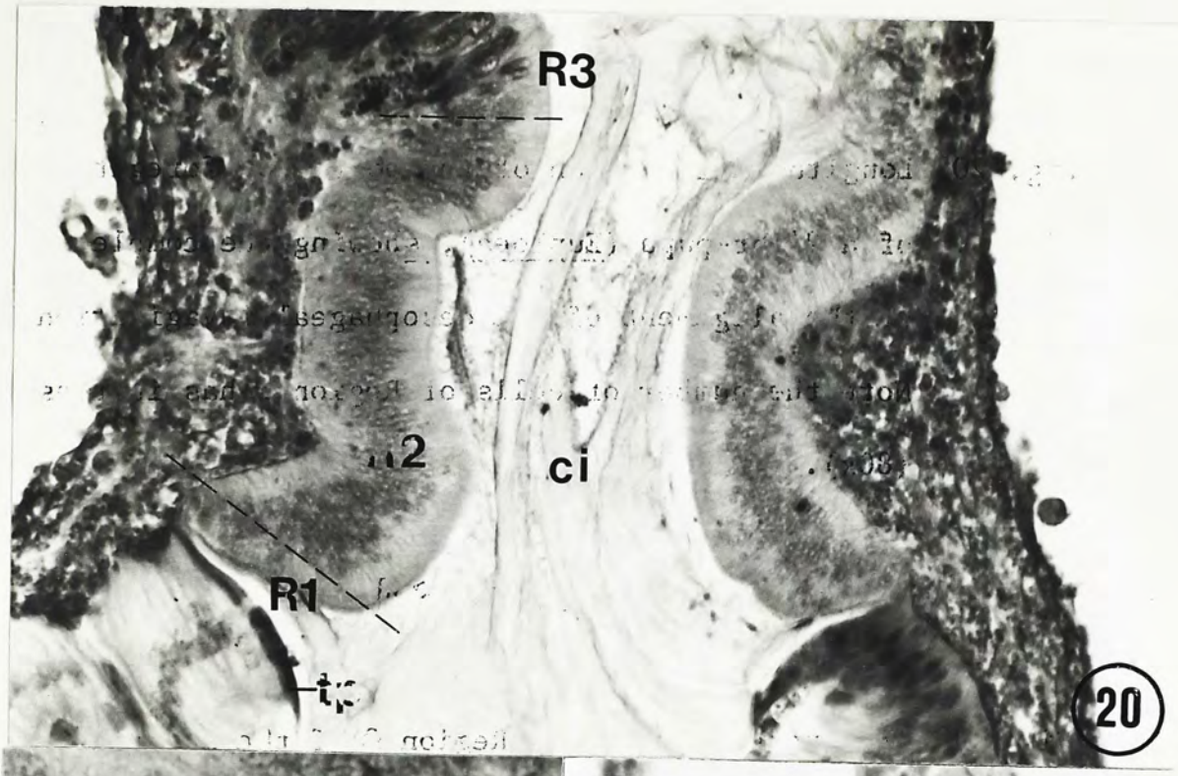
Fig. 20 Longitudinal section of the posterior foregut of a 24-hr-pupa (Euploea), showing the completion of the alignment of the oesophageal invagination. Note the number of cells of Region 2 has increased (80x).

Fig. 21 Transverse section of Region 2 of the anterior imaginal ring of a 30-hr-pupa (Euploea), showing mitotic figures of Region 2 (800x).

Fig. 22 Longitudinal section of the posterior foregut of a 35-hr-pupa (Euploea), showing the primary development of the adult crop. Note the globular bodies which indicate the degeneration of Regions 4 and 5 as well as the outer-lying muscles (200x).


R3
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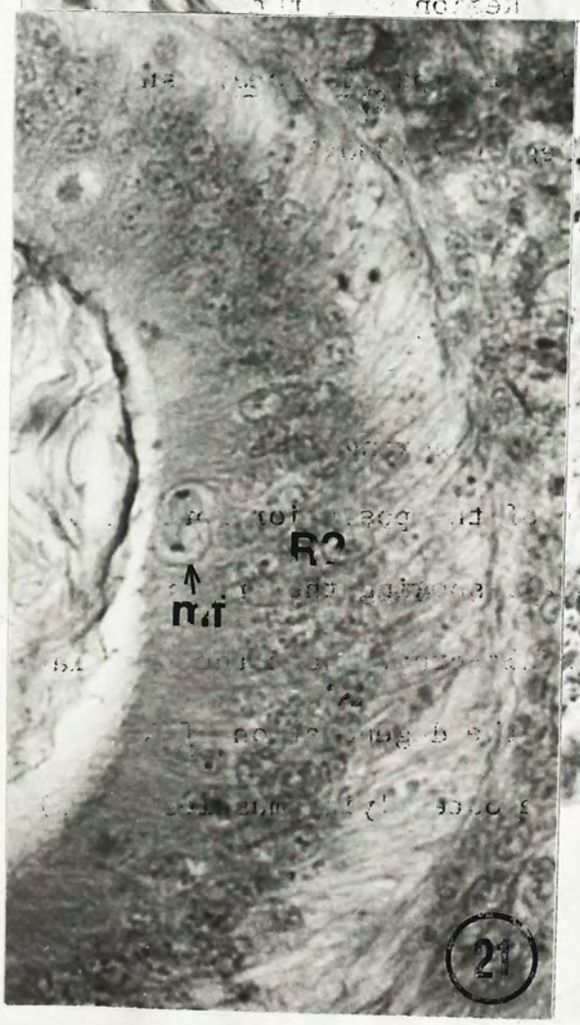
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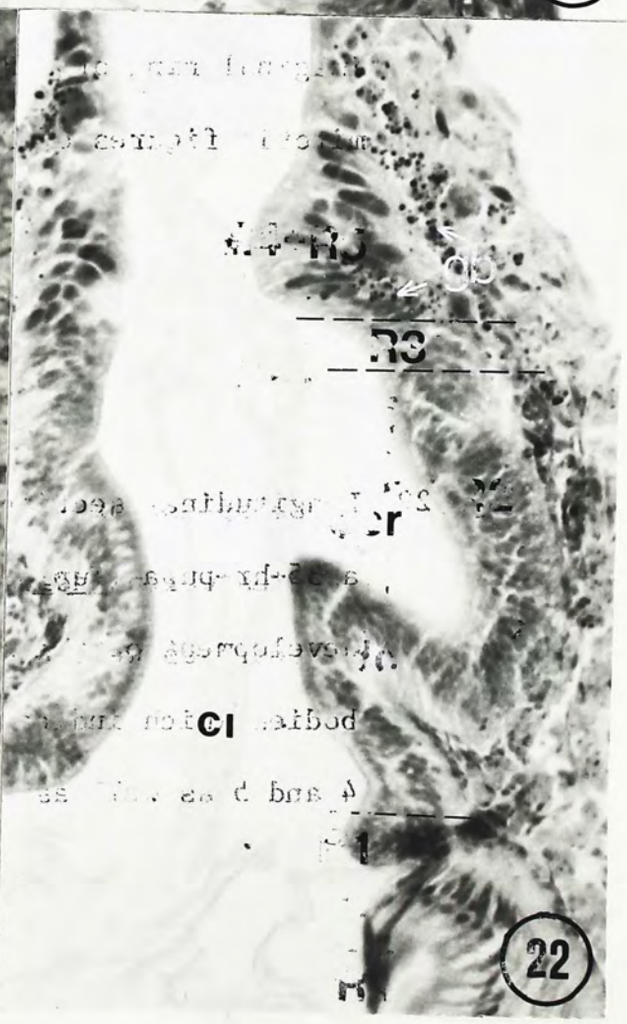
R3
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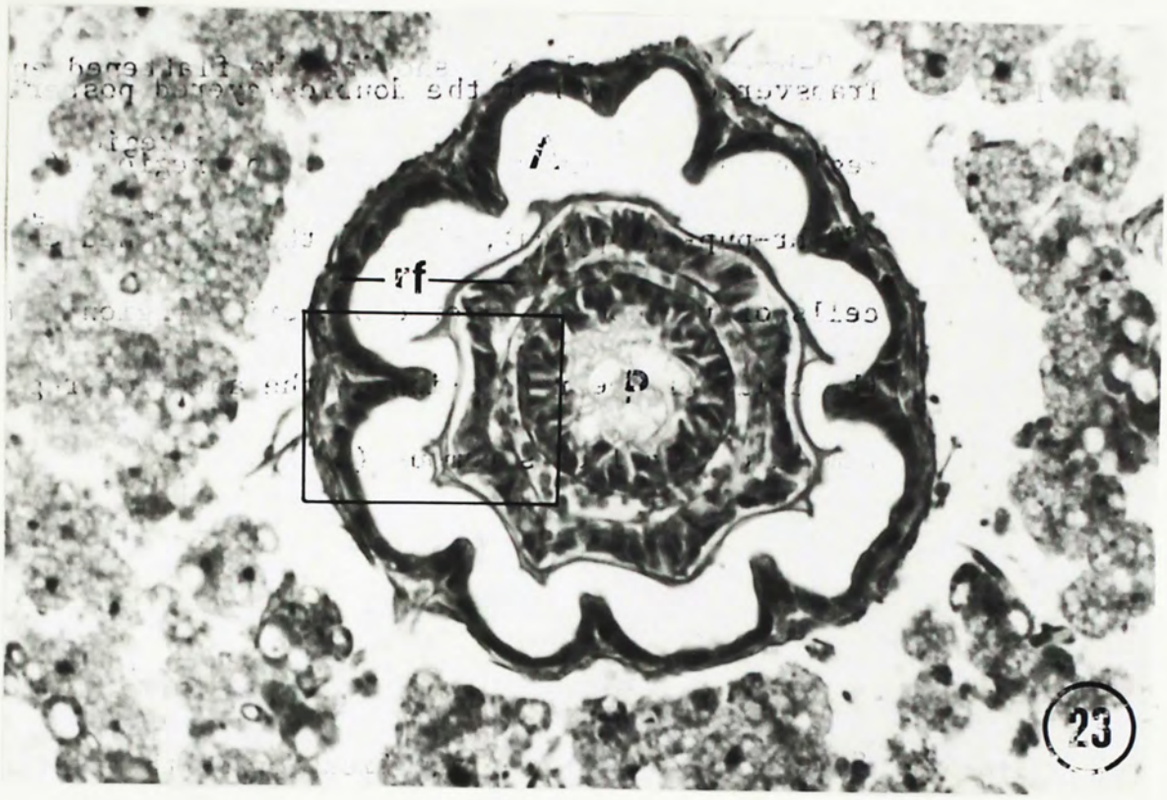
Fig. 23 Transverse section of the double-layered posterior region and the outer folded anterior region of a 220-hr-pupa (Euploea), showing the flattened epithelial cells of the double-layered posterior region. Note the cells of the reflection of the anterior region remain cuboidal or squamous (200x).

Fig. 24 Same as above. High magnification of the rectangular region in Fig. 23 (800x).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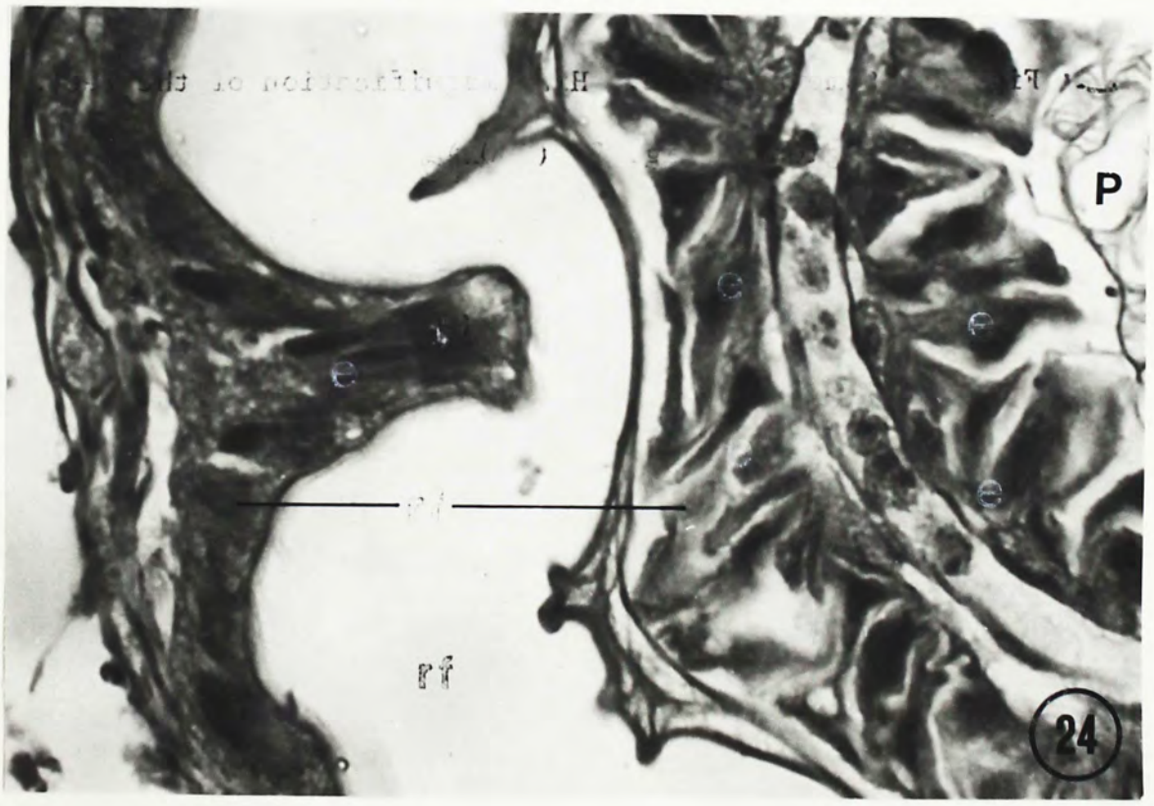
P
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Fig. 25 Longitudinal section of the posterior foregut of a 240-hr-pupa (Euploea), showing the deep reflection of the anterior region (80x).

Fig. 26 Longitudinal section of the posterior foregut of a newly emerged adult (Euploea), showing the proventriculus and the adult oesophageal invagination. Note the adult oesophageal invagination is formed by folding the double-layered wall of the posterior region posteriorly into the midgut (80x).

Fig. 27 Longitudinal section of the posterior foregut of an old adult (Euploea), showing the formation of peritrophic membrane (arrowed). Note the peritrophic membrane is originated from a row of cells at the anterior end of the midgut (80x).


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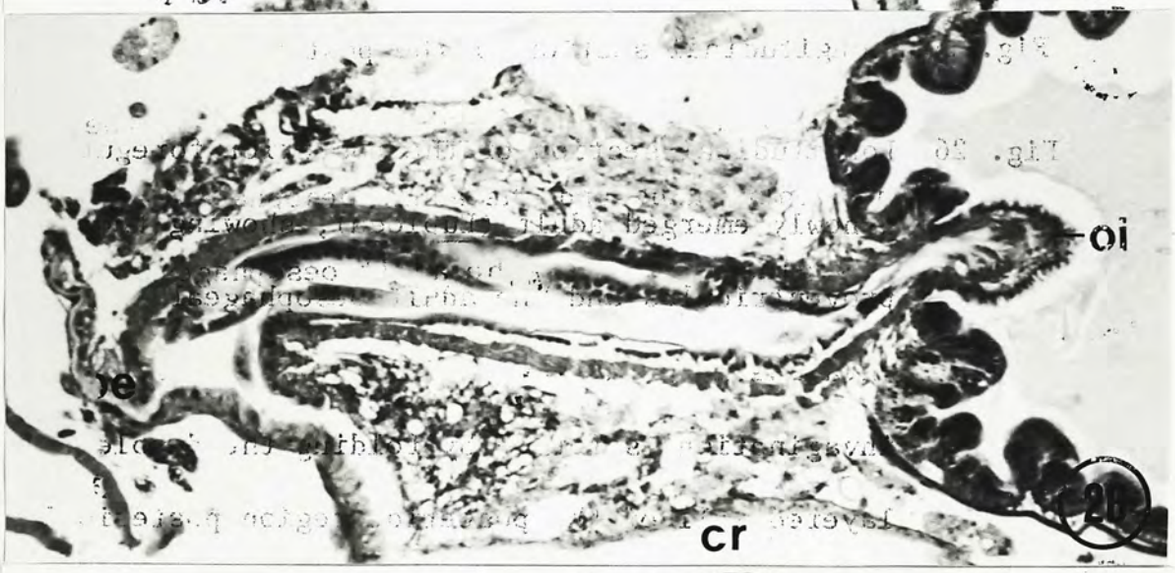
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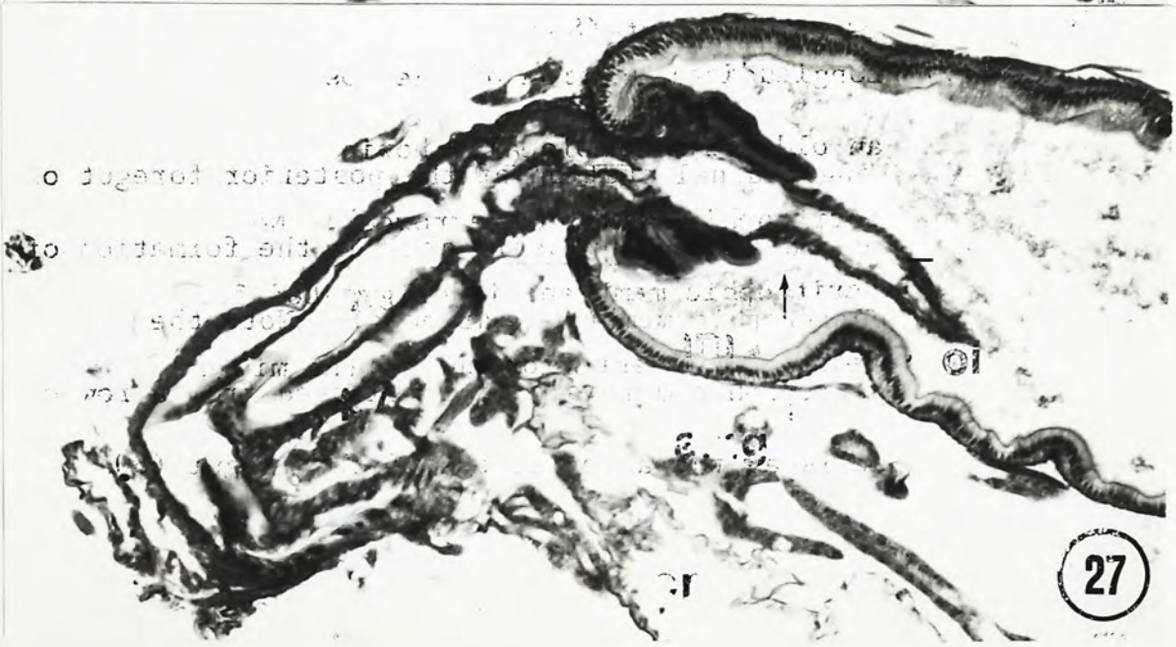
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Fig. 28 Transverse section of the adult crop of Erionota, showing the cytoplasmic projections of the large squamous cells which are situated at the entrance of the crop (800x).

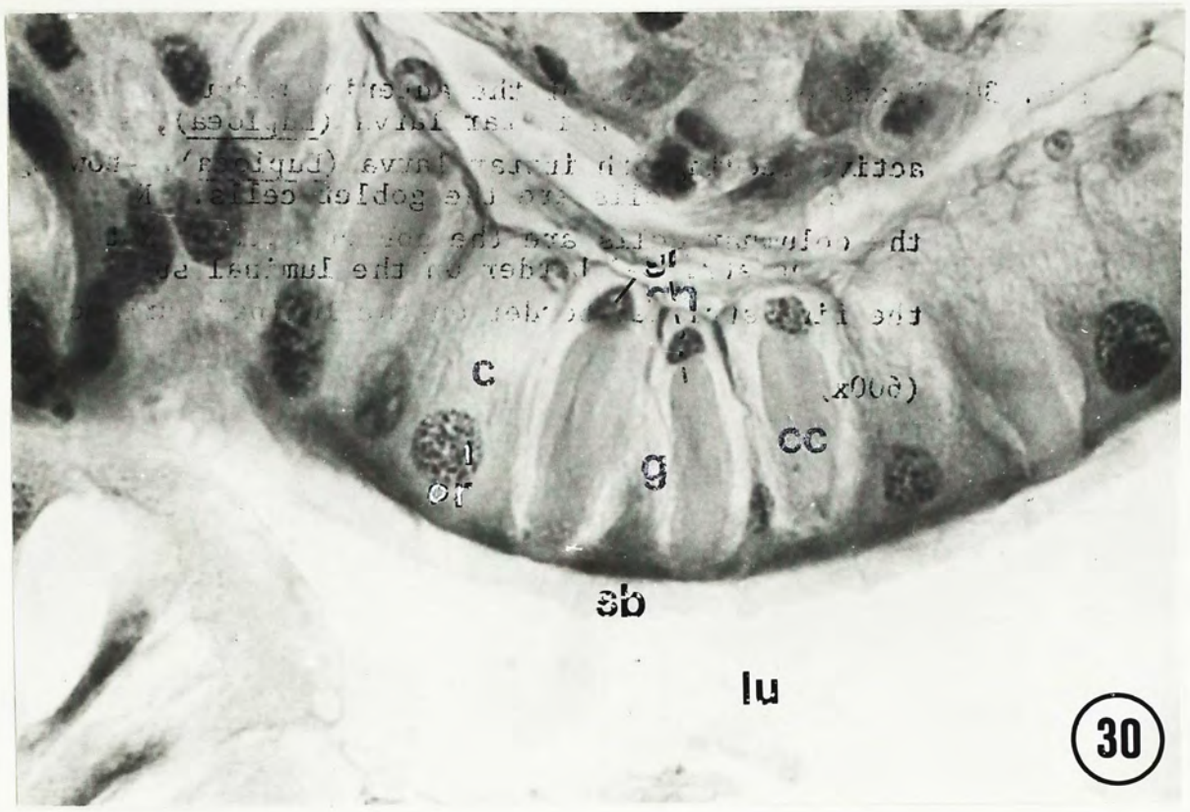
Fig. 29 Transverse section of the adult crop of Erionota, showing the squamous cells with large nuclei (800x).

28

29

Fig. 30 Transverse section of the anterior midgut of an active feeding 5th instar larva (Euploea), showing the columnar cells are the goblet cells. Note the fine striated border on the luminal surface (600x).

Fig. 31 Transverse section of the anterior midgut of an active feeding 5th instar larva (Euploea), showing the delamination of the midgut. As a result, the peritrophic membrane is formed (400x).



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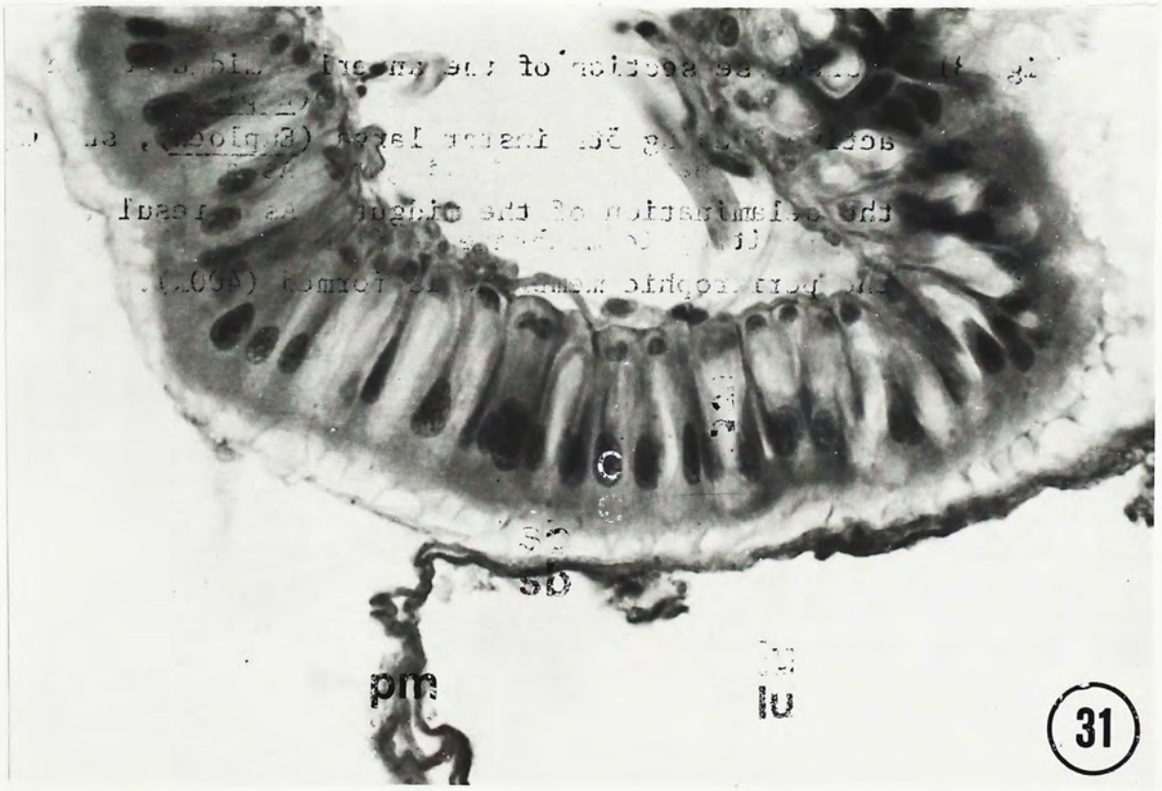

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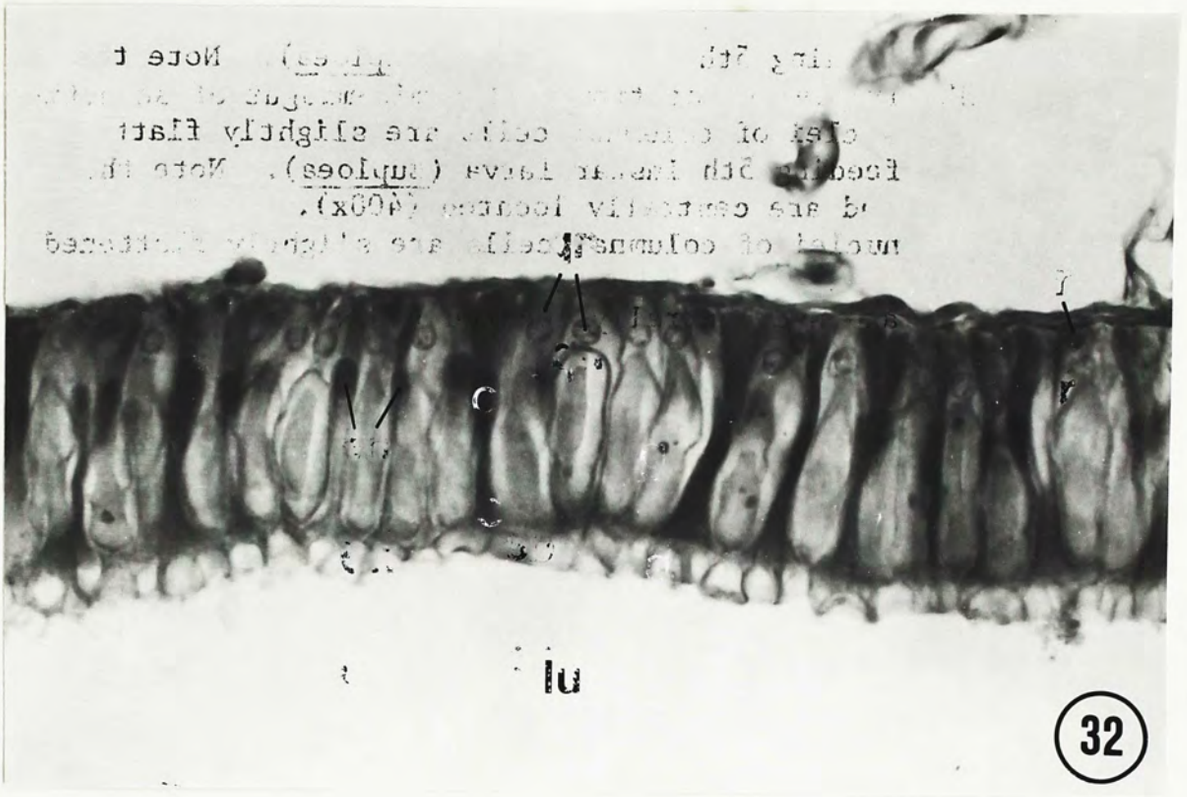
Fig. 32 Transverse section of the mid-midgut of an active feeding 5th instar larva (Euploea). Note the nuclei of columnar cells are slightly flattened and are centrally located (400x).

Fig. 33 Longitudinal section of the posterior midgut of and active feeding 5th instar larva (Euploea), showing the vesicles extruded from the epithelium (80x).



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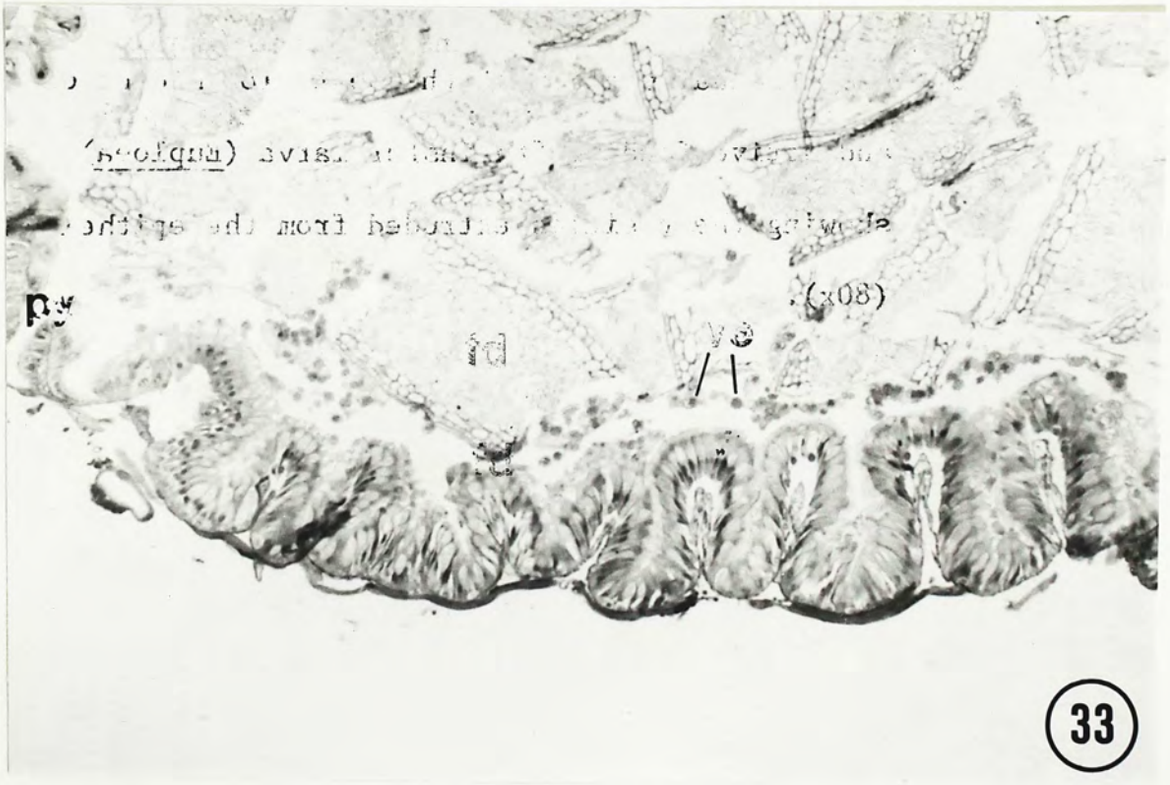

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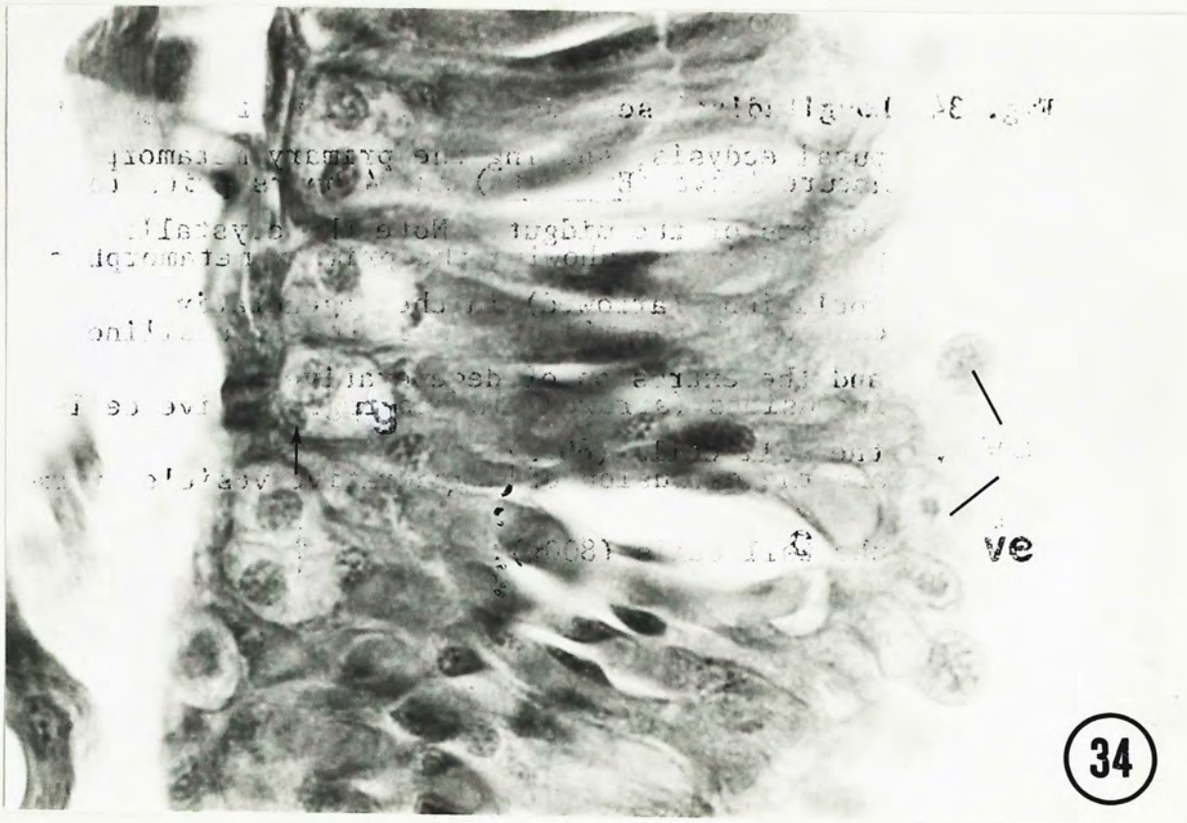
Fig. 34 Longitudinal section of the anterior midgut of a mature larva (Erionota) at 24 hours prior to pupal ecdysis, showing the primary metamorphic changes of the midgut. Note the crystalline inclusions (arrowed) in the degenerative cells and the extrusion of degenerative vesicles from the tall cells (800x).

Fig. 35 Transverse section of the mid-midgut of a mature larva (Erionota) at 12 hours prior to pupal ecdysis. The characteristics of the tall cells become obscure (800x).



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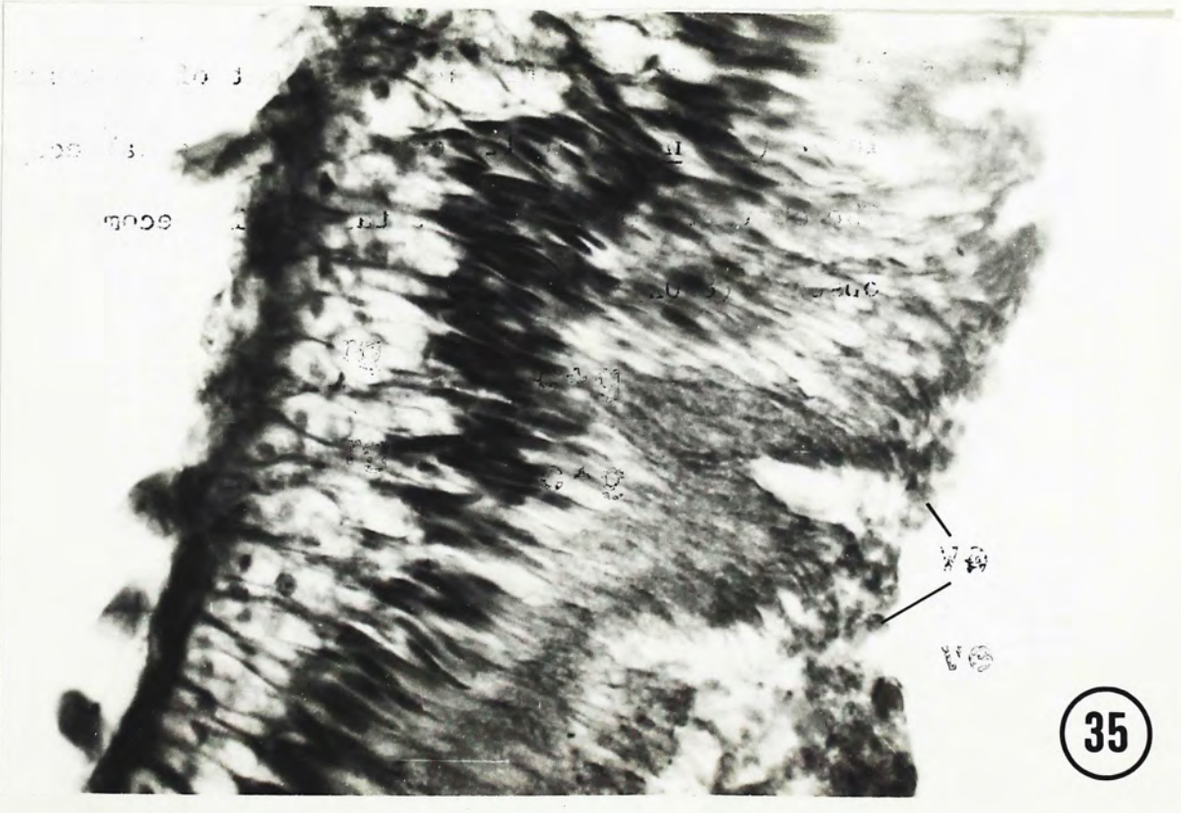

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Fig. 36 Transverse section of the anterior midgut of a mature larva (Erionota) at a few hours prior to pupal ecdysis, showing the replacement of the larval epithelium by the pupal epithelium. Note the folded larval epithelium or the yellow body which is sloughed to the lumen. The larval striated border is still evident (arrowed) (200x).

Fig. 37 Longitudinal section of the mid-midgut of a 0-hr-pupa (Erionota), showing the extrusion of vesicles to the lumen (200x).


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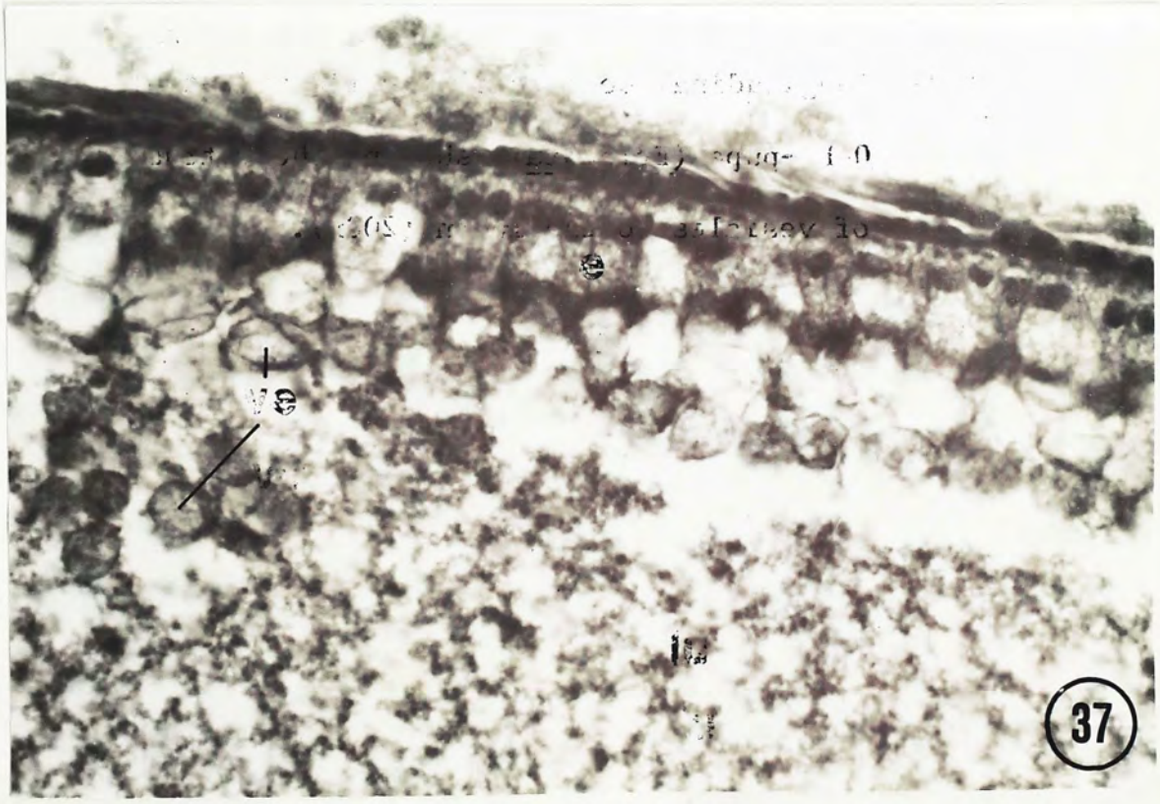
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Fig. 38 Longitudinal section of the mid-midgut of a 45-hr-pupa (Erionota), showing the pupal regenerative cell (400x).

Fig. 39 Longitudinal section of the midgut of a 150-hr-pupa (Erionota), showing the elongated columnar cells of the midgut. Note the extrusion of vesicles (arrowed) (400x).

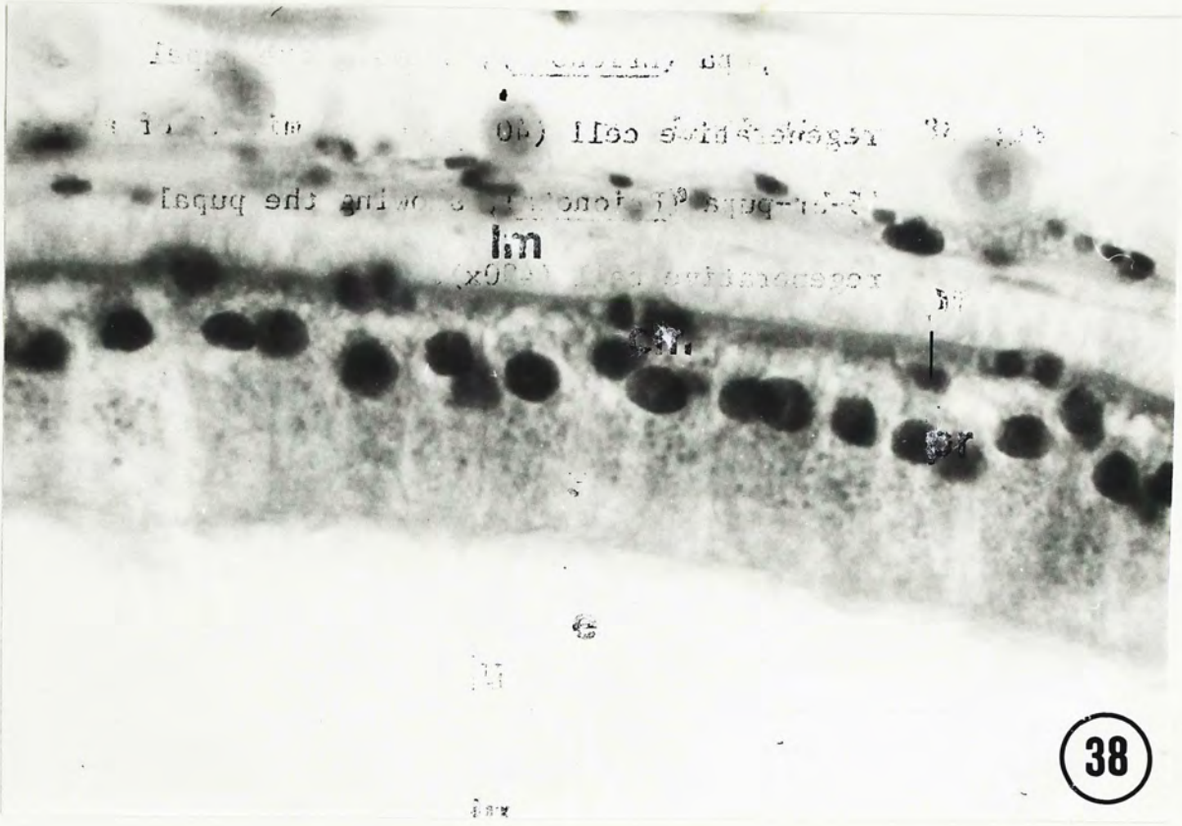

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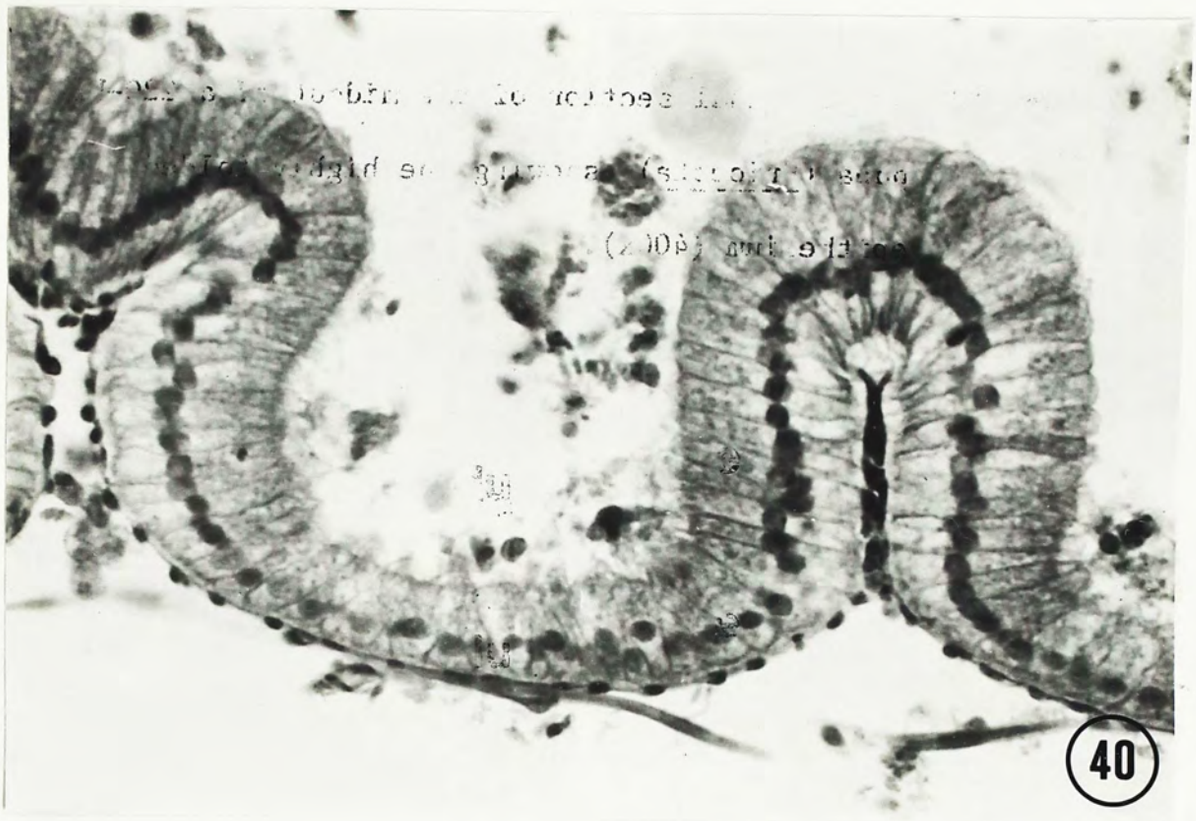
Fig. 40 Longitudinal section of the midgut of a 220-hr-pupa (Erionota), showing the highly folded epithelium (400x).

Fig. 41 Transverse section of the adult midgut of Erionota. Note the epithelial cells become club-shaped. The striated border retains its fine appearance (800x).



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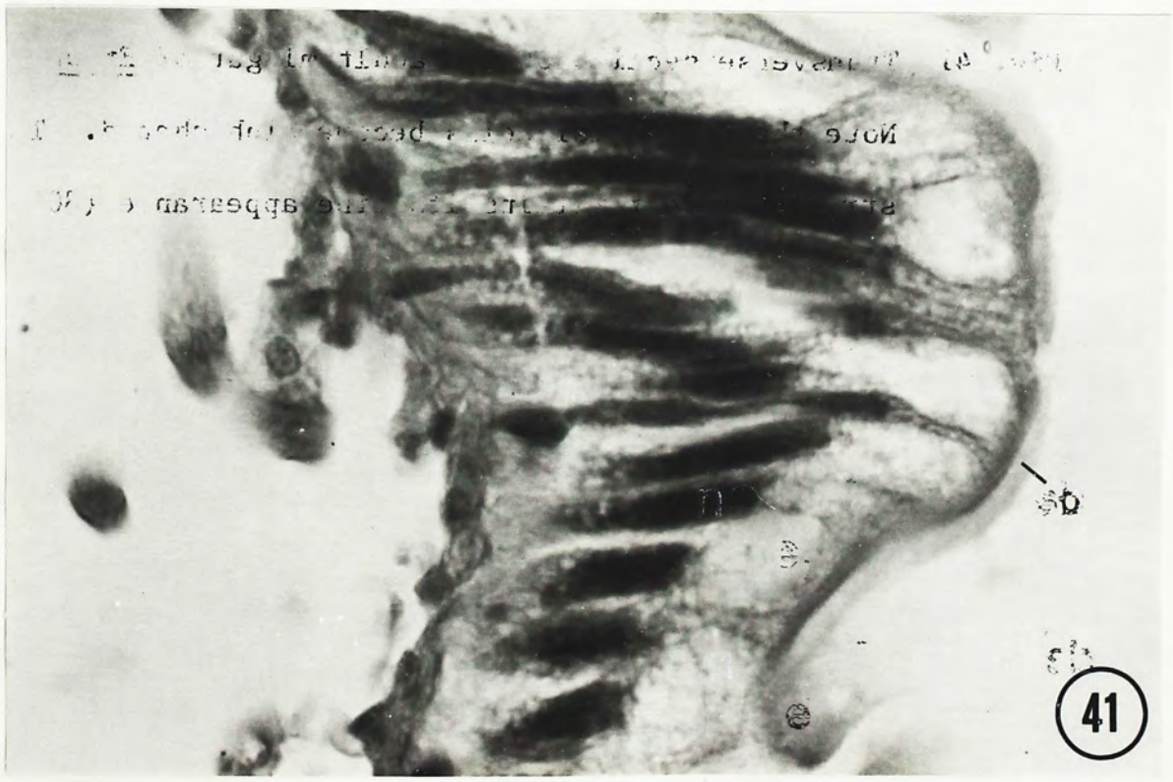

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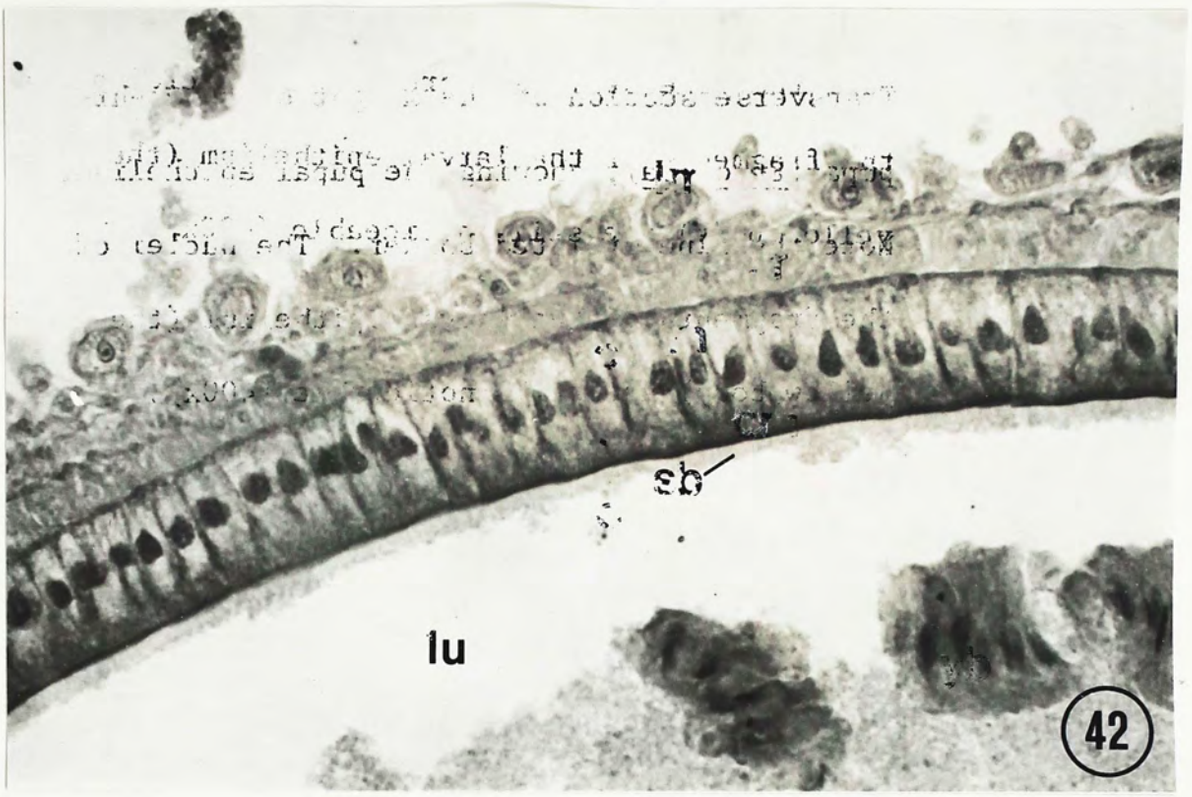
Fig. 42 Transverse section of the midgut of a 105-hr-pupa (Eriongta), showing the pupal epithelium. Note the fine striated border. The nuclei of the fragments of the larval epithelium (the yellow body) are still noticeable (400x).

Fig. 43 Longitudinal section of the midgut of a 240-hr-pupa (Euploea). Note the active secretion of the columnar cells (400x).



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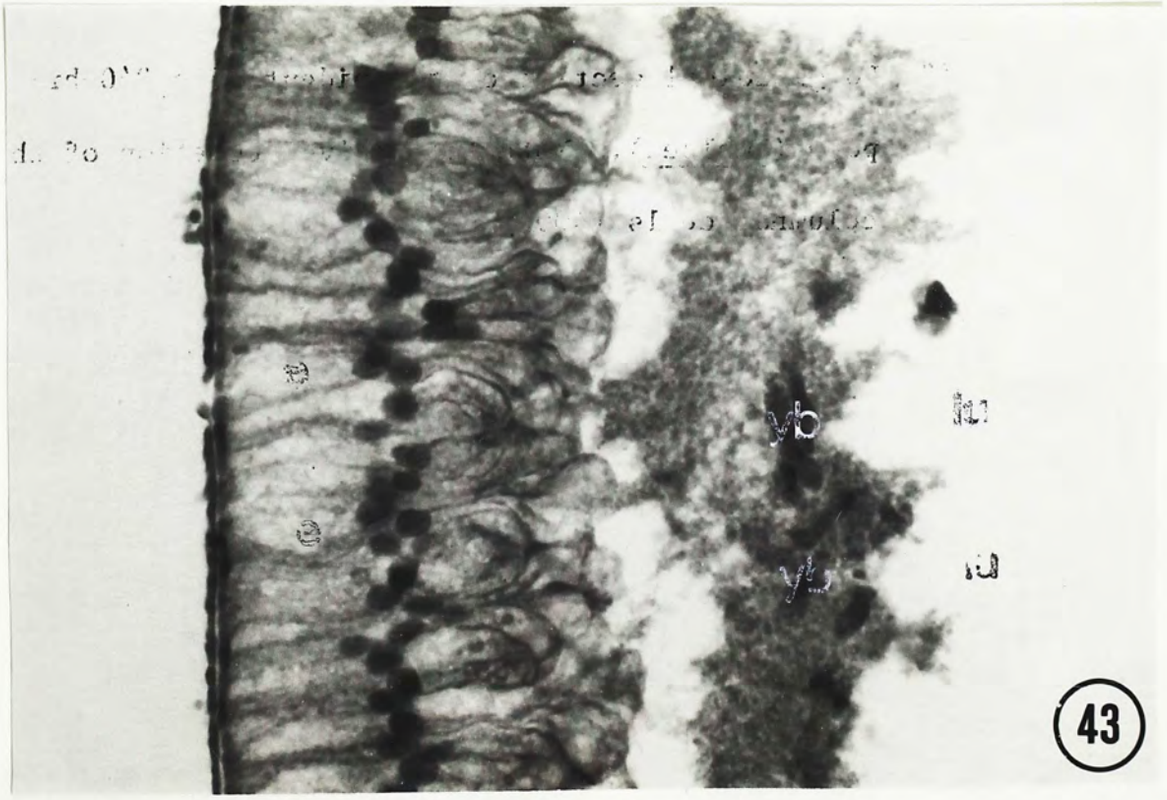

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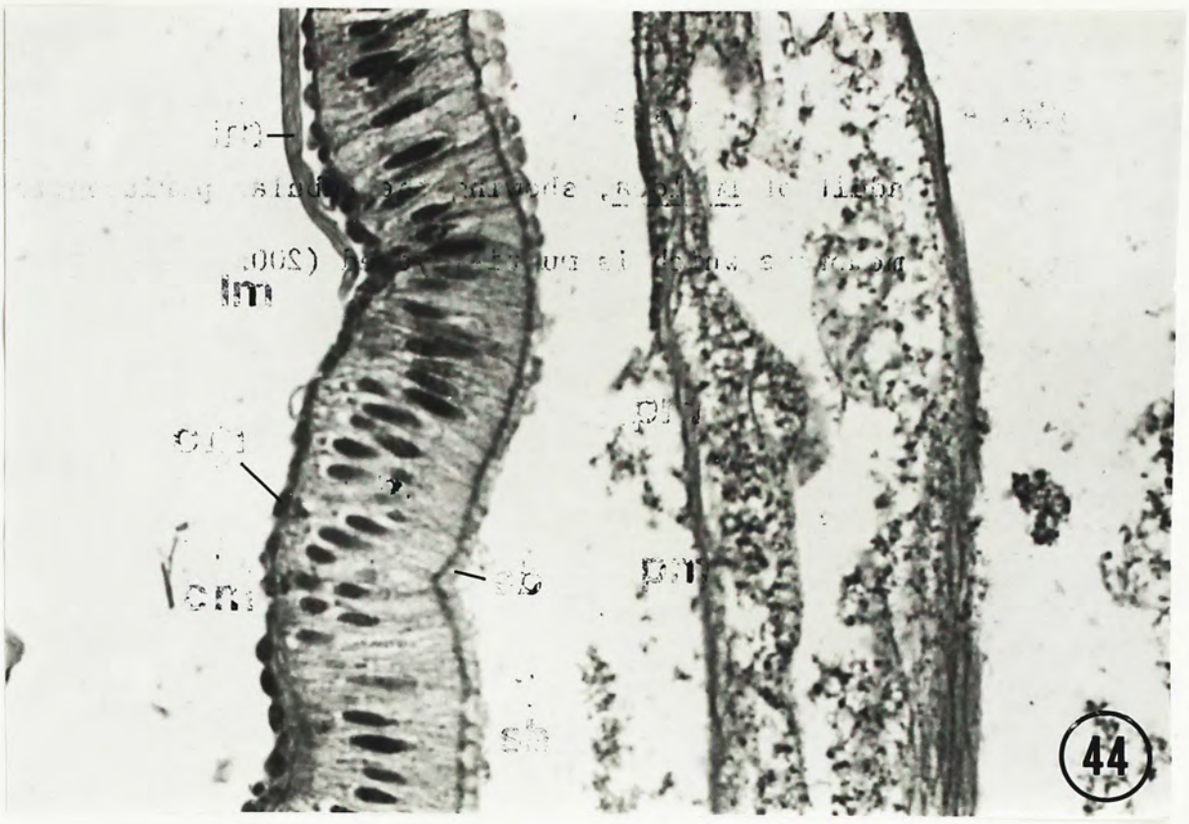
Fig. 44 Longitudinal section of the midgut of an old adult of Euploea, showing the tubular peritrophic membrane which is multi-layered (200x).

Fig. 45 Longitudinal section of the pylorus of an active feeding 5th instar larva (Euploea), showing the posterior imaginal ring (pi), the pyloric cone (pc), and the protuberance. Note the protuberance is composed of columnar cells. The anterior half of the protuberance is covered with smooth intima, and the posterior half is covered with spiculated intima (200x).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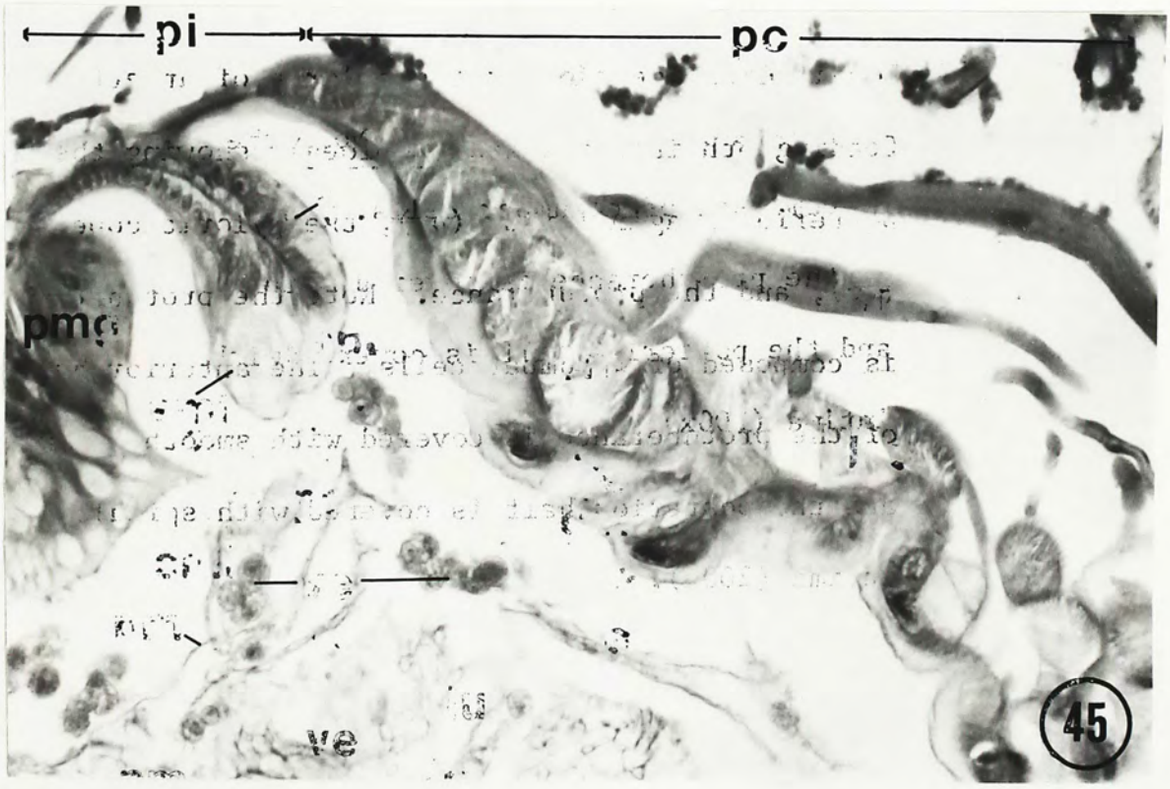
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Fig. 46 Longitudinal section of the anterior part of the pyloric valve of an active feeding 5th instar larva (Euploea), showing the spiculated intima ring cells on the anterior end of the pyloric valve (200x).

Fig. 47 Transverse section of the pyloric valve of an active feeding 5th instar larva (Euploea). Note the ring of the thick circular sphincter muscles (sm) and the epithelial lobes occluding the lumen. (80x).


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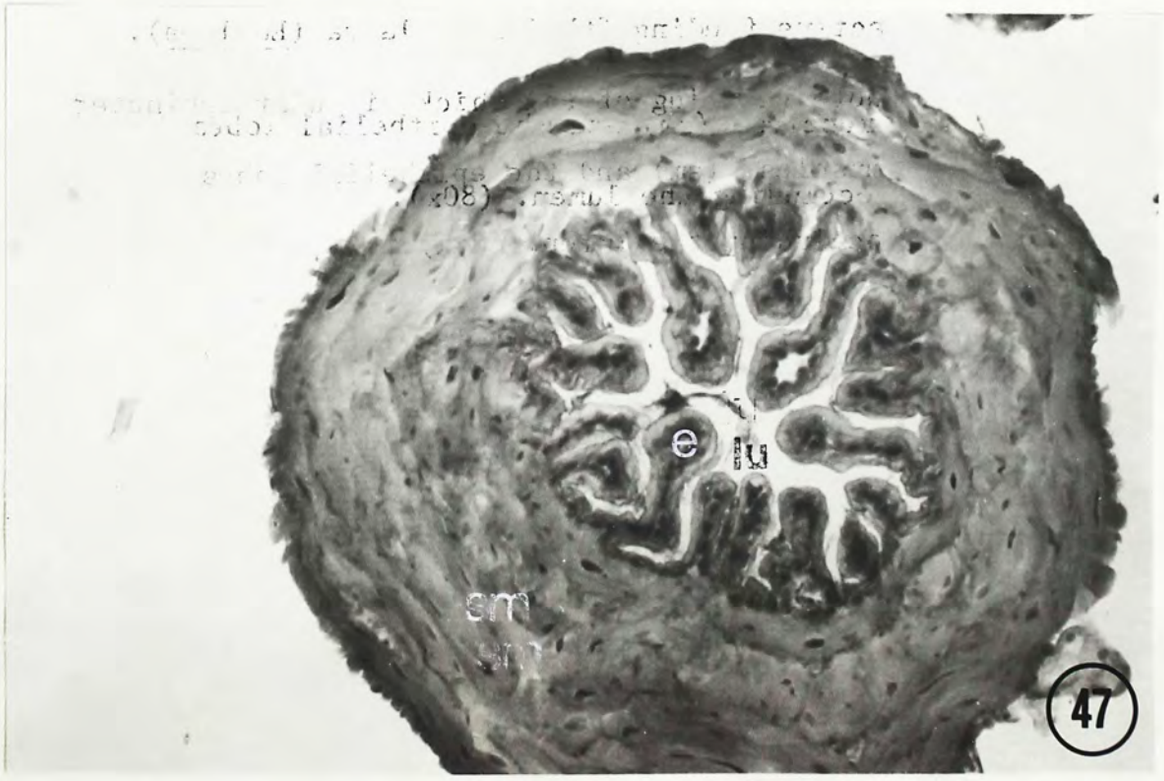
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Fig. 48 Transverse section of the ileum of an active feeding 5th instar larva (Erionota). Note the folded epithelium (200x).

Fig. 49 Transverse section through the posterior region of the sphincter of an active feeding 5th instar larva (Euploea), showing the convoluted epithelium which is lined with thick cuticular intima. Note there is no ileonode or giant epithelial cell present in the ilial epithelium (80x).

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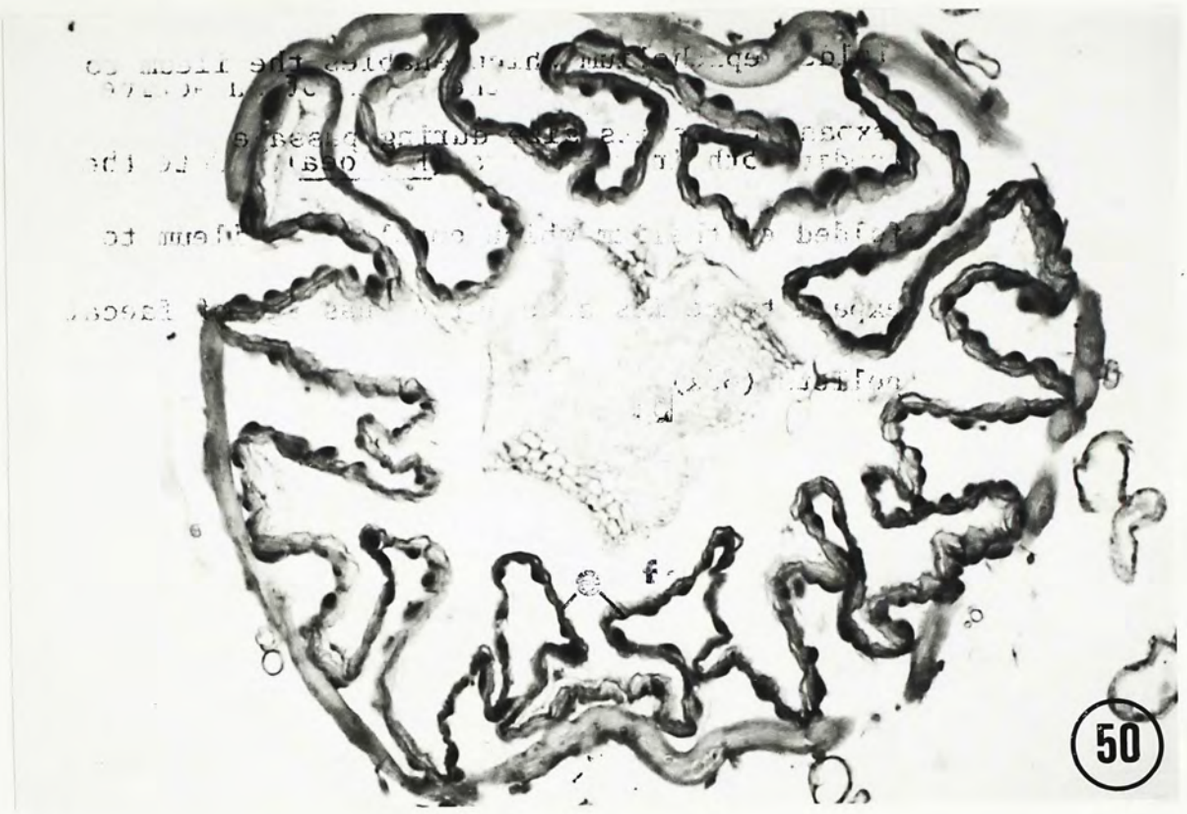
Fig. 50 Transverse section of the ileum of an active feeding 5th instar larva (Euploea). Note the folded epithelium which enables the ileum to expand twice its size during passage of faecal pellets (80x).

Fig. 51 Longitudinal section through the border between the rectal valve and the rectal sac of an feeding 5th instar larva (Erionota). Note the sclerotized ring (sr) that marks the anterior end of the rectal sac. The rectal complex is apparently noticeable (200x).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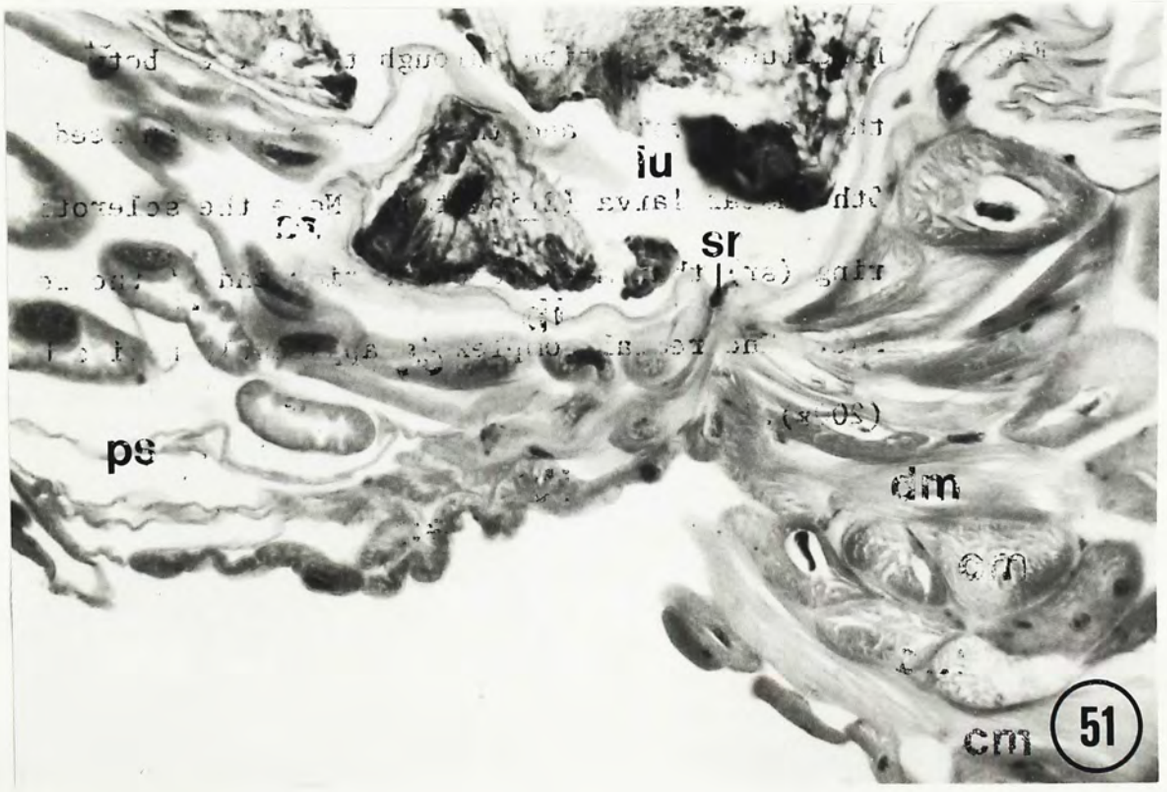
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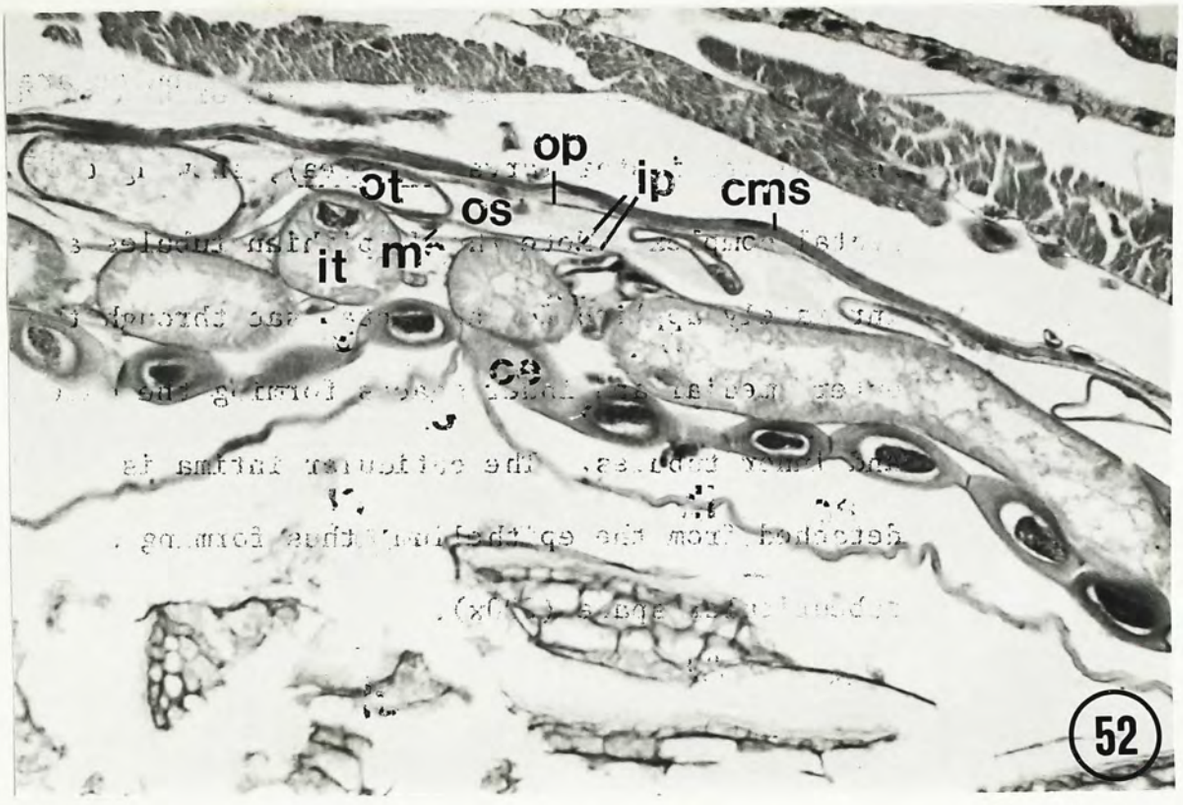
Fig. 52 Transverse section of the rectal sac of an active feeding 5th instar larva (Euploea), showing the rectal complex. Note the Malpighian tubules are intimately applied to the rectal sac through the outer, medial and inner spaces forming the outer and inner tubules. The cuticular intima is detached from the epithelium, thus forming a subcuticular space (200x).

Fig. 53 Transverse section through the posterior end of the rectal complex of an active feeding 5th instar larva (Euploea), showing the normal rectal epithelium (ne). Note the cells of the epithelium are in contact with the cuticular intima. There is no reassociation of Malpighian tubules on the outer surface of the epithelial wall (200x).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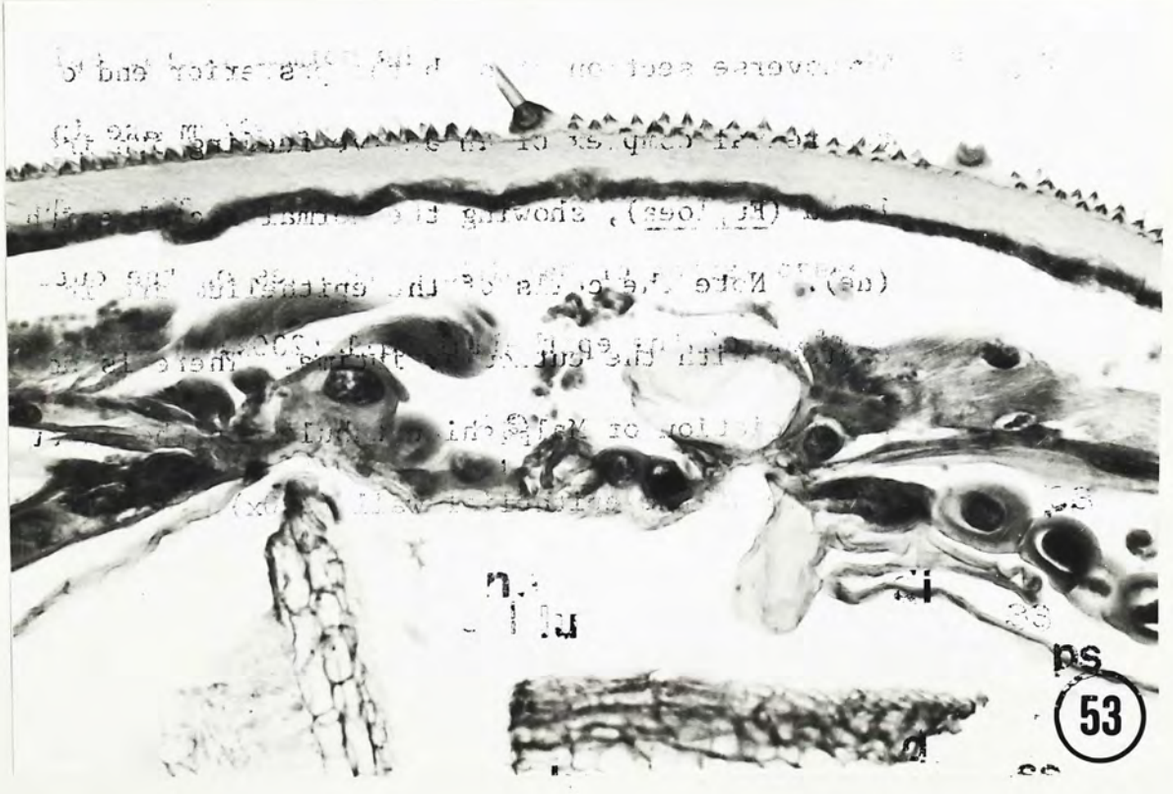
ps
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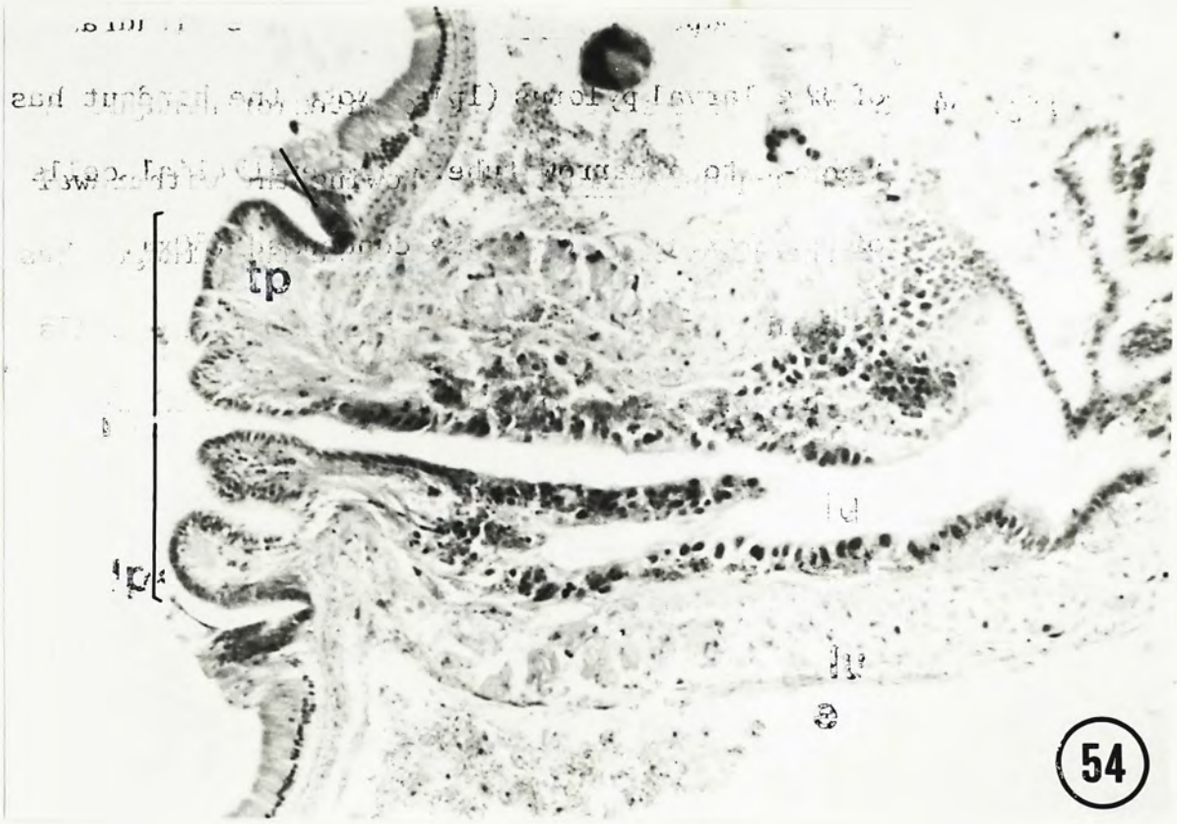
Fig. 54 Longitudinal section of the anterior hindgut of a 30-hr-pupa (Erionota), showing the withdrawal of the larval pylorus (lp). Note the hindgut has reduced to a narrow tube. The epithelial cells of the larval pylorus are condensed (80x).

Fig. 55 Longitudinal section of the anterior hindgut of a 50-hr-pupa (Erionota), PAS stained, showing the degeneration of the outer-lying muscles. Note the globular bodies (arrowed) stained darkly with PAS. The musculature of the midgut persists its composition throughout the insect's life (200x).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tp
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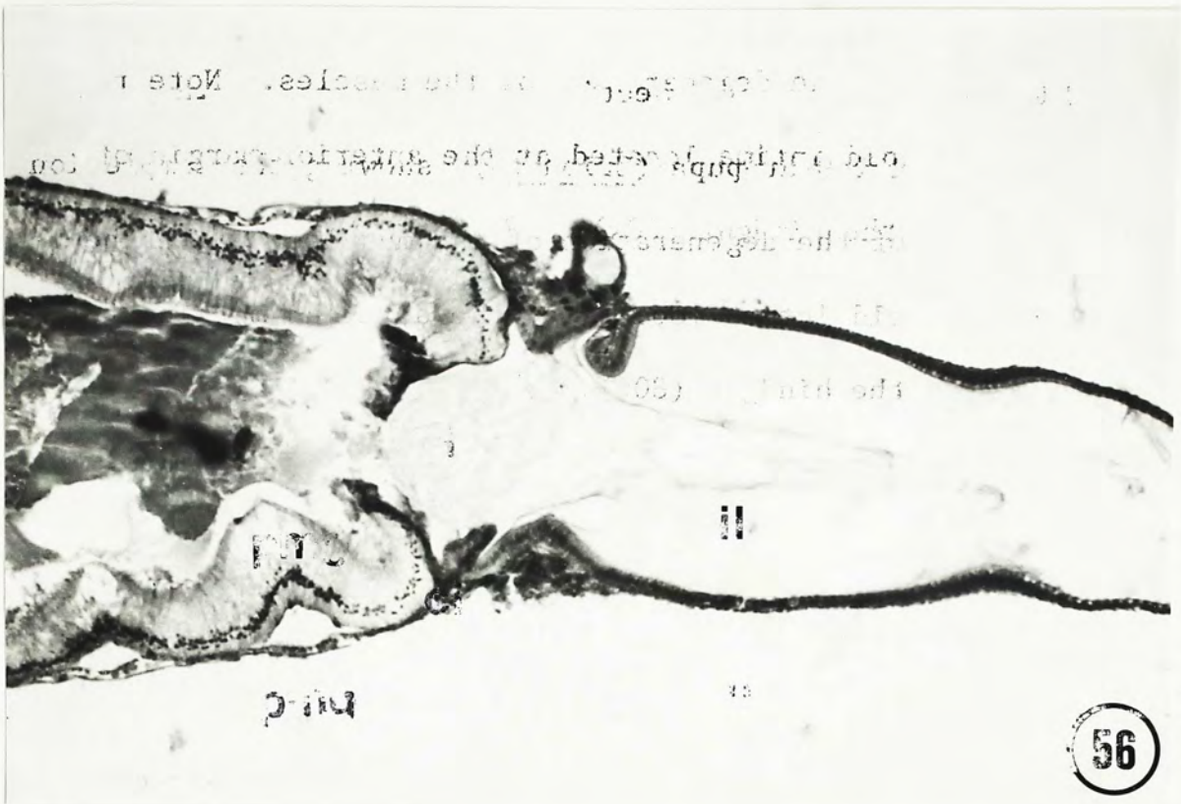
Fig. 56 Longitudinal section of the anterior hindgut of a 180-hr-pupa (Erionota), showing the completion of the degeneration of the muscles. Note the old intima located at the anterior margin of the hindgut (80x).

Fig. 57 Longitudinal section of the anterior hindgut of a 240-hr-pupa (Erionota), showing the discharge of the waste products from the midgut to the hindgut. The ileum expands twice its size to receive these products (80x).



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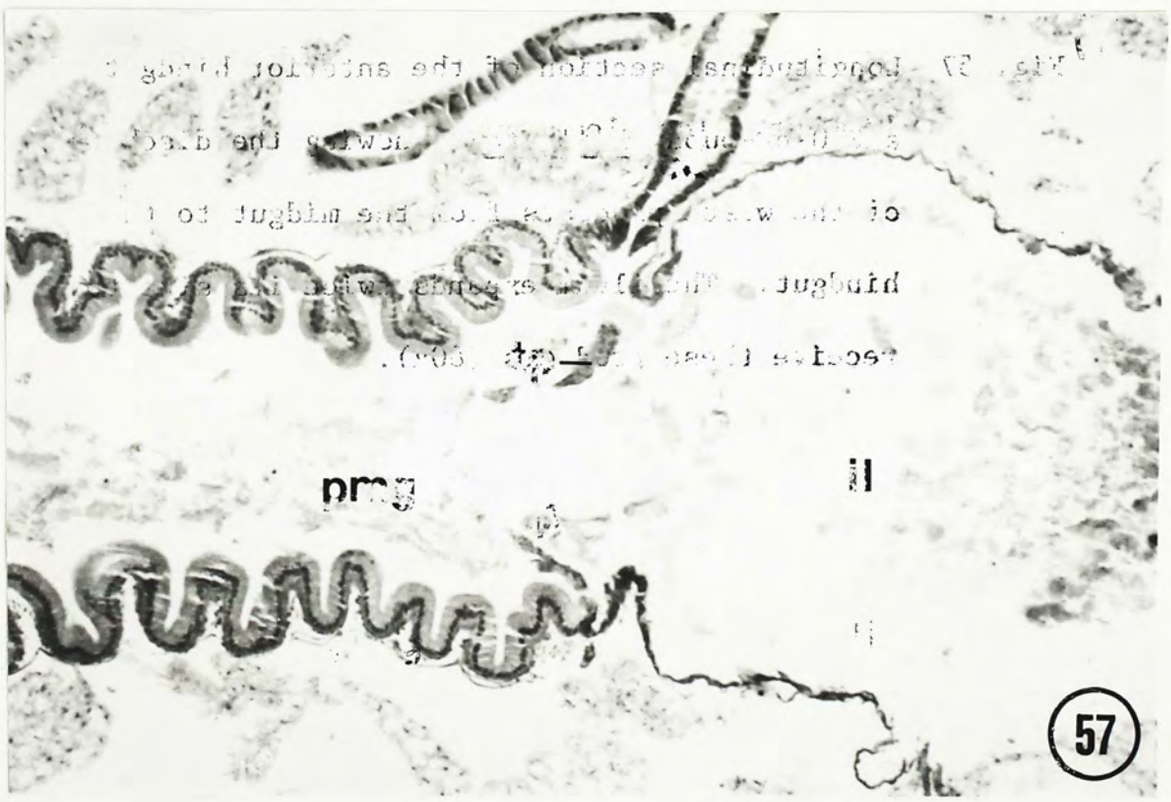

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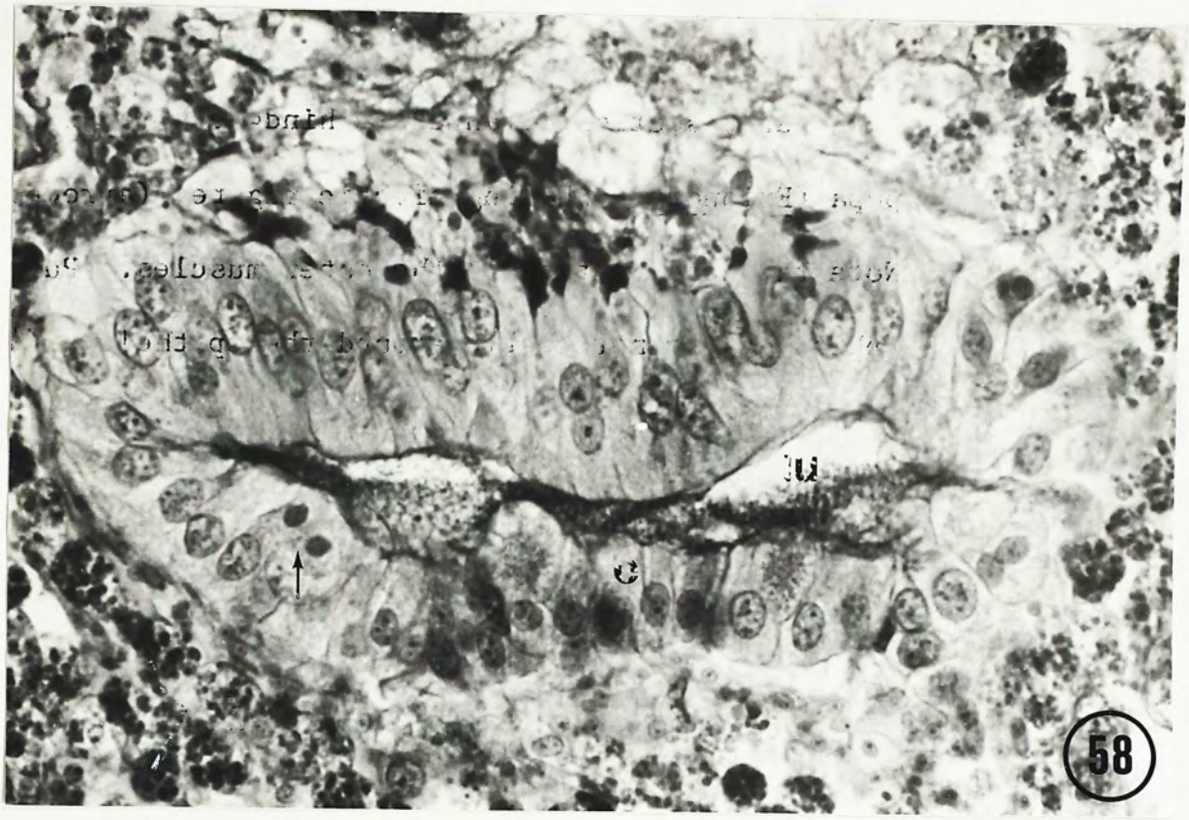
Fig. 58 Transverse section of anterior hindgut of a 50-hr-pupa (Erionota), showing mitotic figures (arrowed). Note the degeneration of the outer muscles. Pupal spherules are noticeable around the epithelium (400x).

Fig. 59 Longitudinal section of the pupal ileum of a 150-hr-pupa (Euploea), showing the highly folded epithelium (200x).



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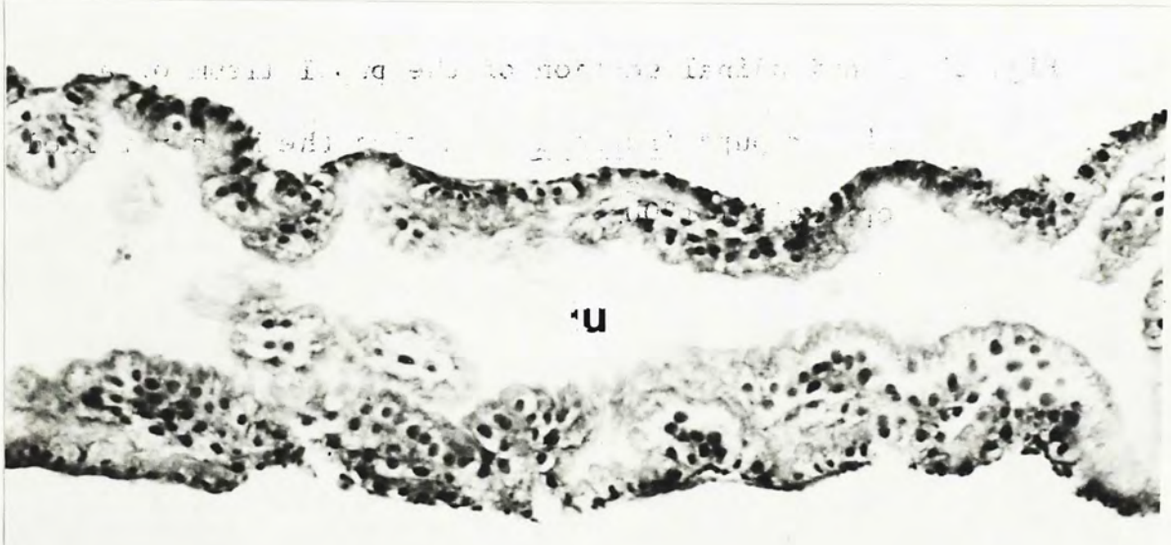

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Fig. 60 Longitudinal section of the pupal ileum of a 200-hr-pupa (Euploea), showing the deep circular folding of the epithelium (400x).

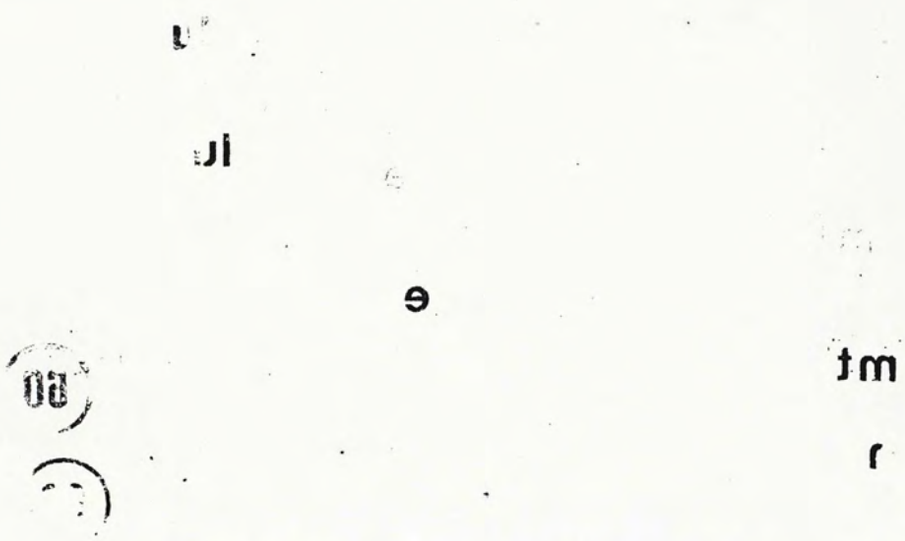
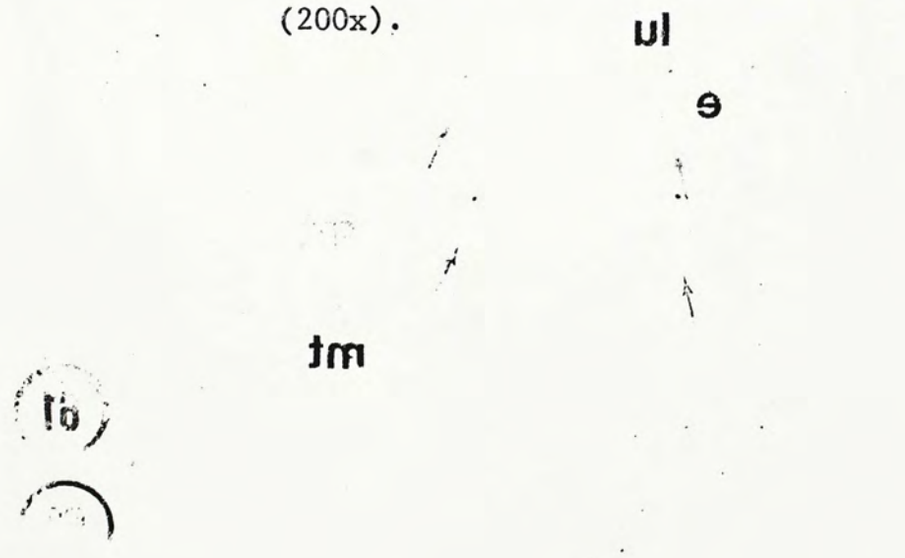


Fig. 61 Transverse section of the pupal ileum of a 240-hr-pupa (Erionota), showing the longitudinal foldings of the epithelium. Note the attach-points of the longitudinal muscles (arrowed) (200x).



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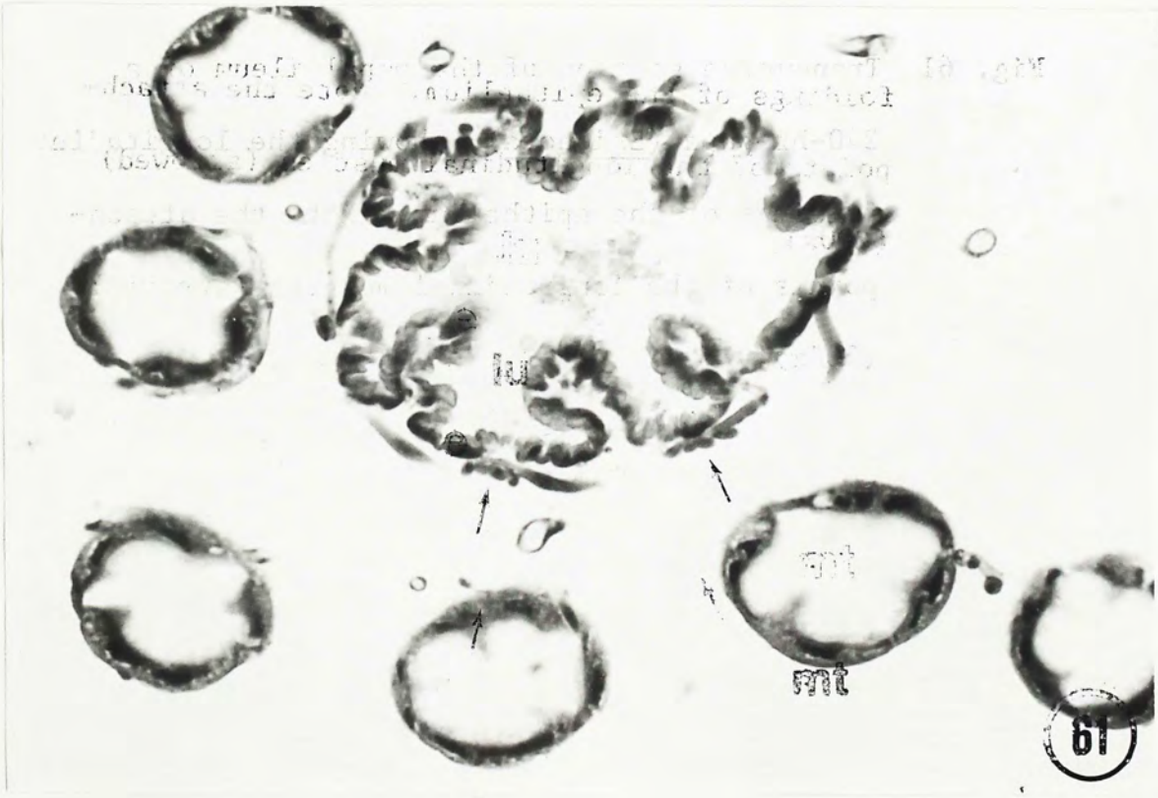

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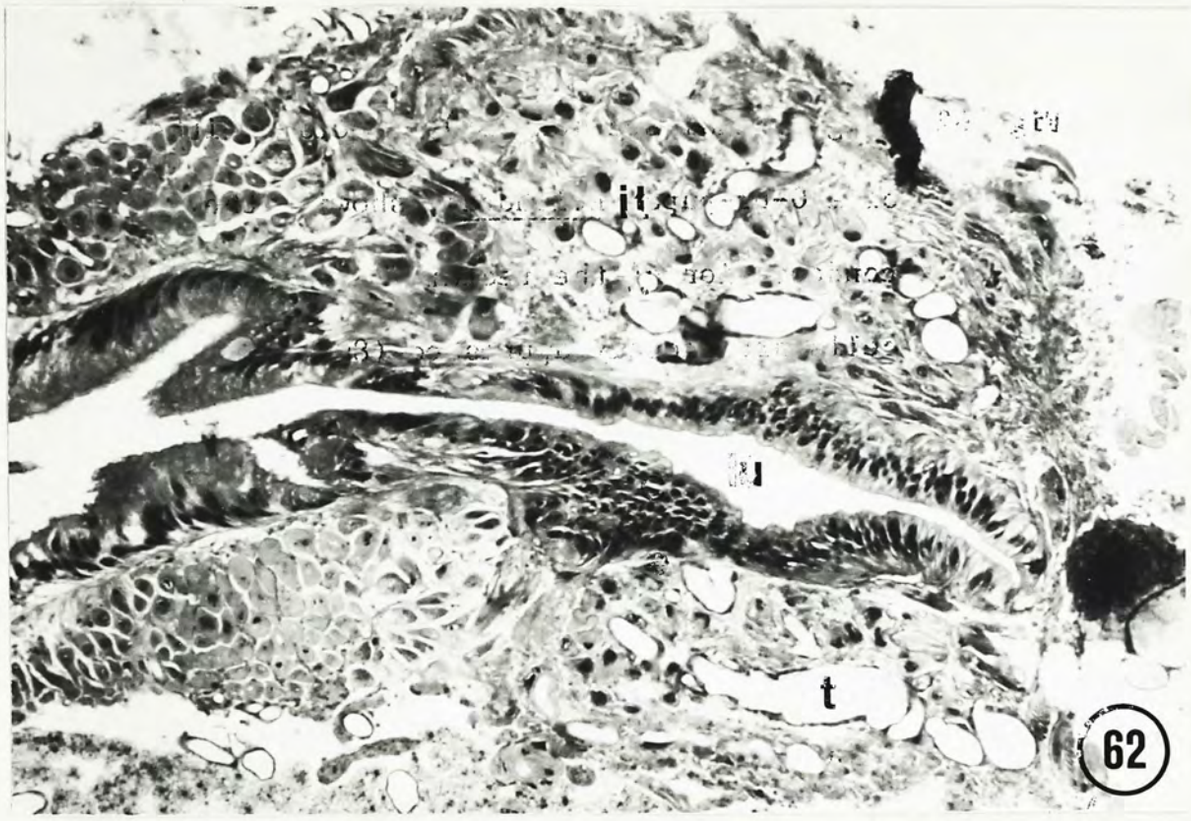
Fig. 62 Longitudinal section of the rectal epithelium of a 0-hr-pupa (Erionota), showing the condensation of the rectum. The epithelial cells are closely appressed (80x).

Fig. 63 Longitudinal section of the rectal epithelium of a 45-hr-pupa (Erionota), showing the dissociation of the rectal complex and the degeneration of the outer muscles (80x).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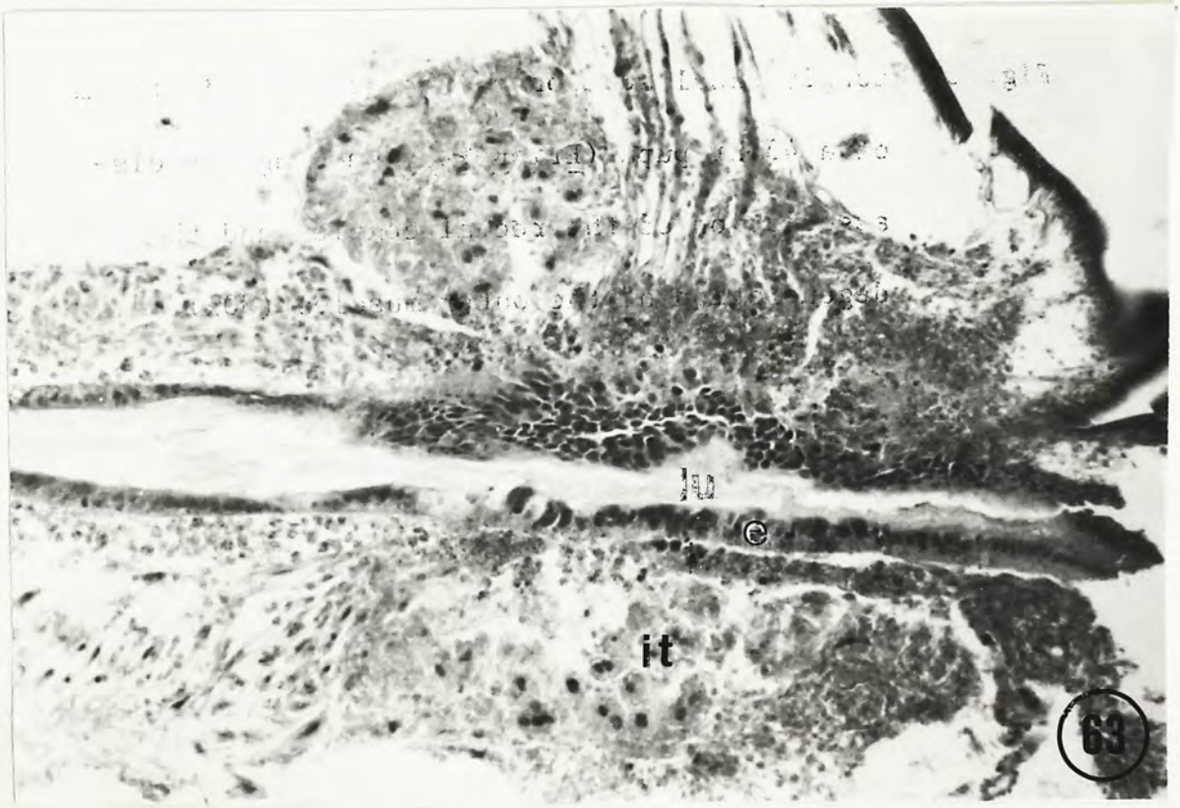
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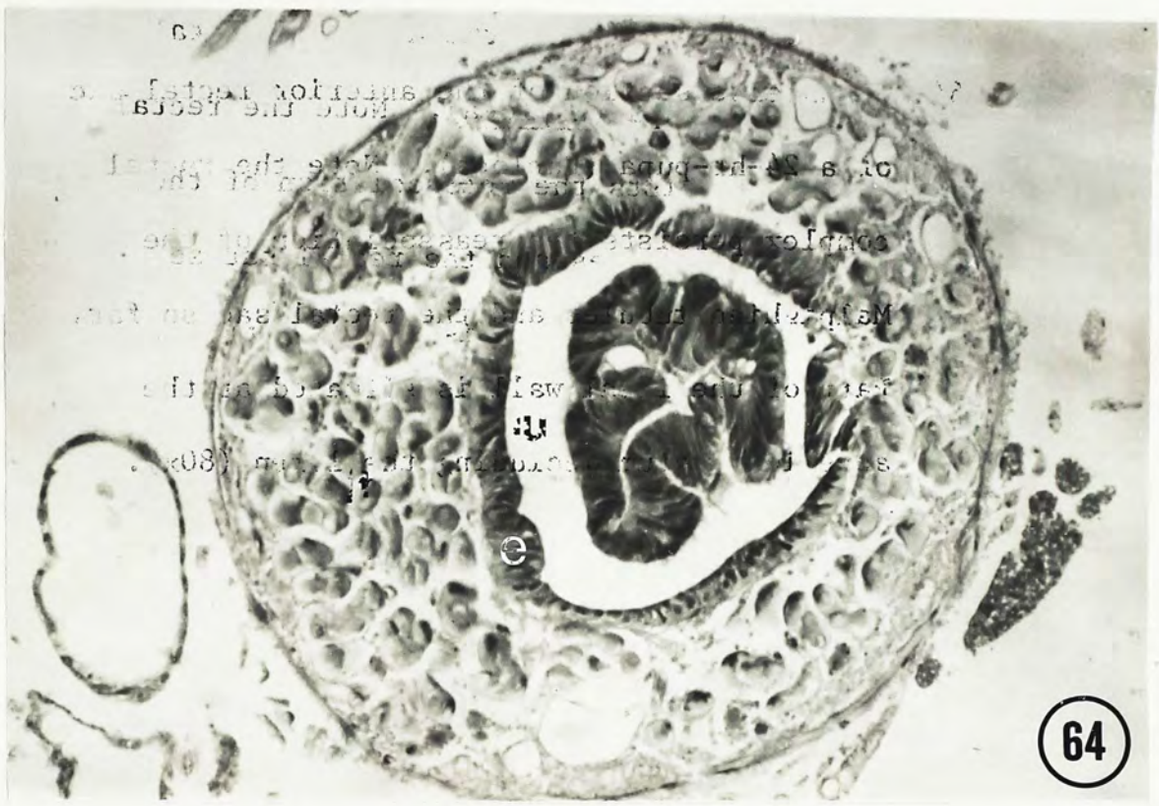
Fig. 64 Transverse section of the anterior rectal sac of a 24-hr-pupa (Euploea). Note the rectal complex persists the reassociation of the Malpighian tubules and the rectal sac so far. Part of the ileal wall is situated at the anterior rectum occluding the lumen (80x).

Fig. 65 Transverse section of the posterior rectal sac of a 24-hr-pupa (Euploea), showing the rectal sac is reduced to a narrow tube with three diverticula (80x).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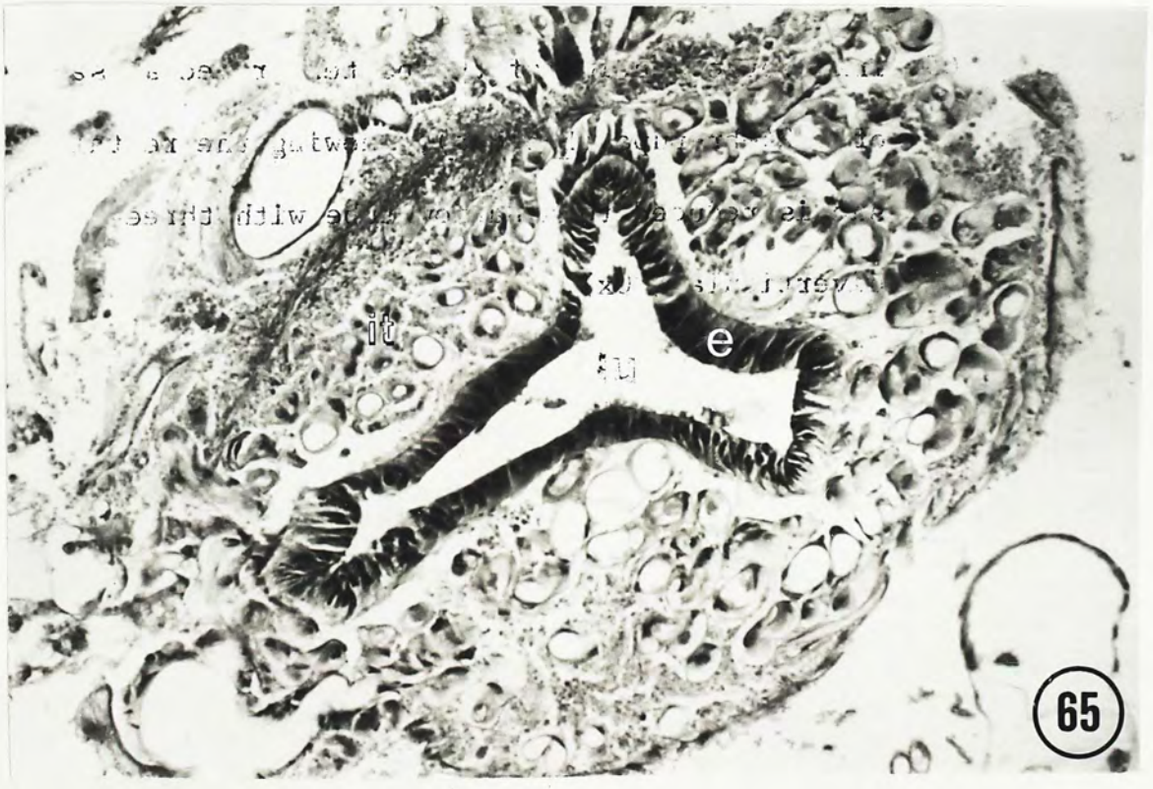
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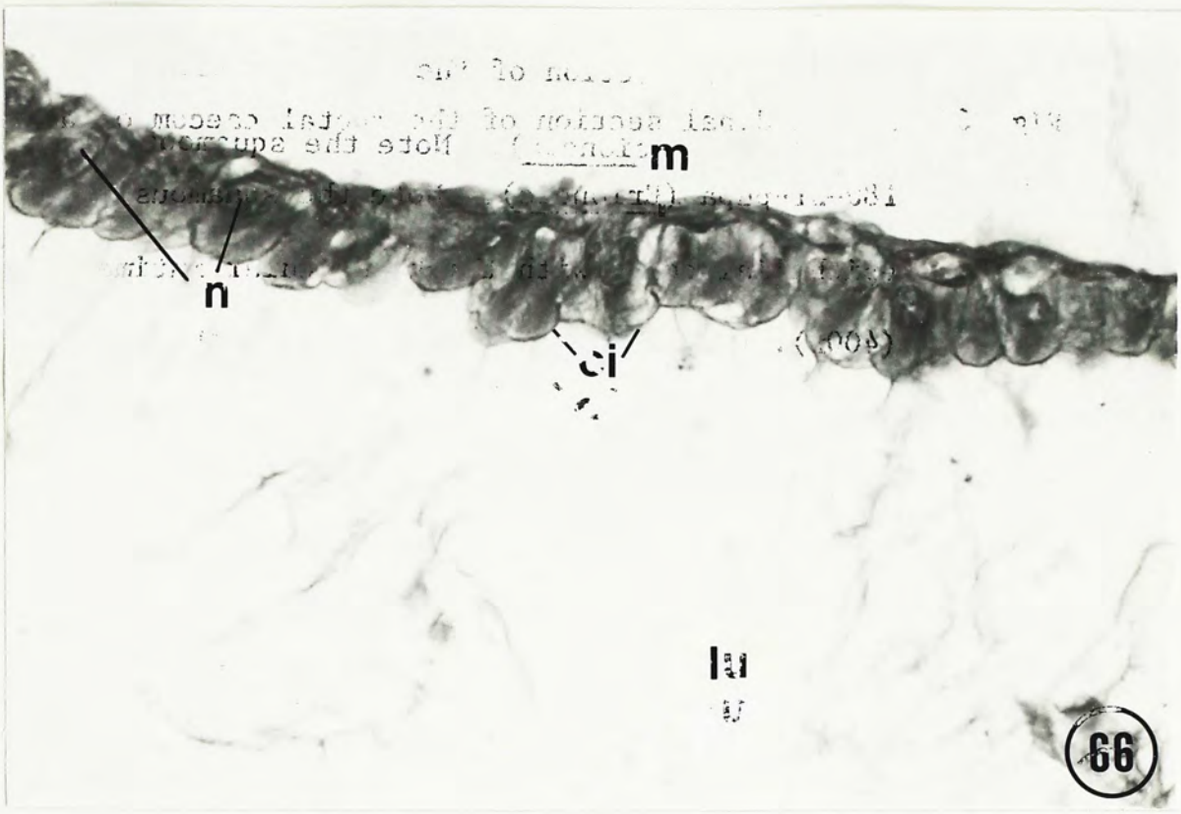
Fig. 66 Longitudinal section of the rectal caecum of a 180-hr-pupa (Erionota). Note the squamous epithelial cells with thick cuticular intima (400x).

Fig. 67 Longitudinal section of the rectal caecum of a 220-hr-pupa (Erionota), showing the highly folded epithelium. Unidentified globular bodies (arrowed) are found in the epithelial cells (400x).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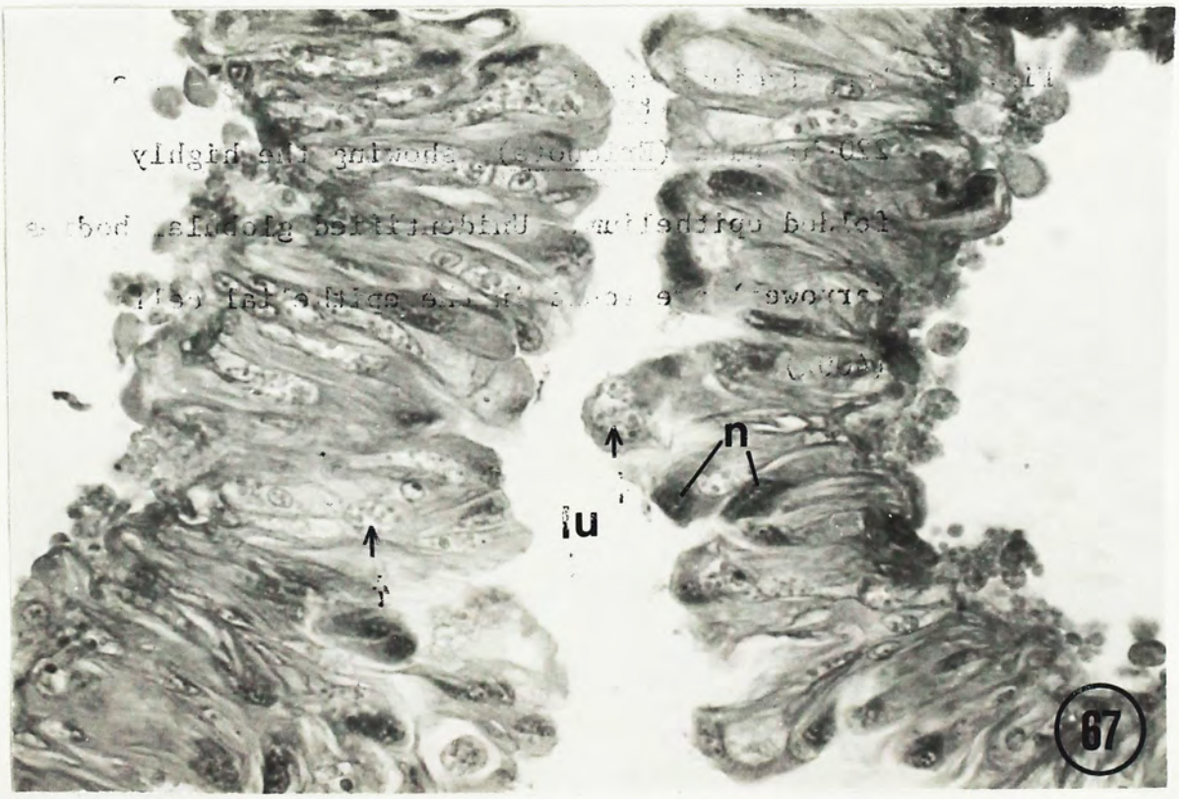
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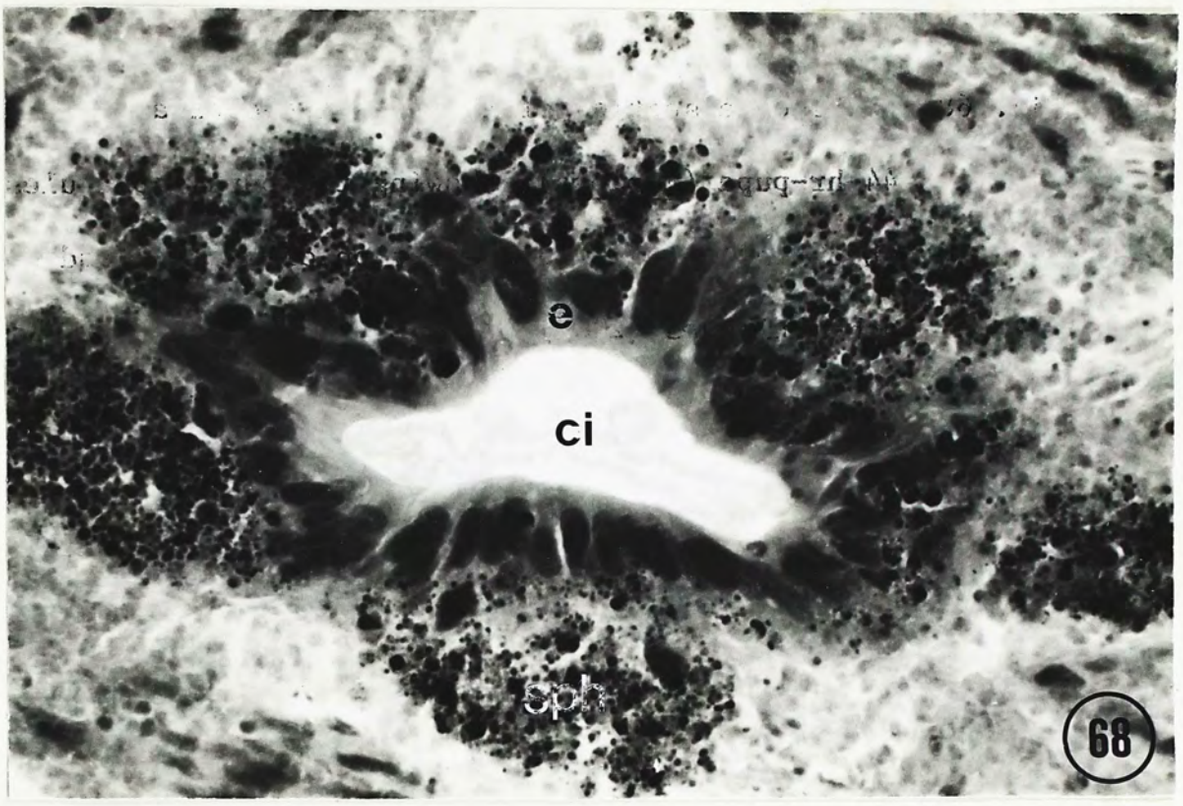
Fig. 68 Transverse section of the rectal sac of a 44-hr-pupa (Euploea), showing the pupal spherules which indicate the degeneration of muscles and other tissues (200x).

Fig. 69 Transverse section of the posterior region of the rectal caecum of a 72-hr-pupa (Erionota), showing the junction where the ileum enters the rectum (200x).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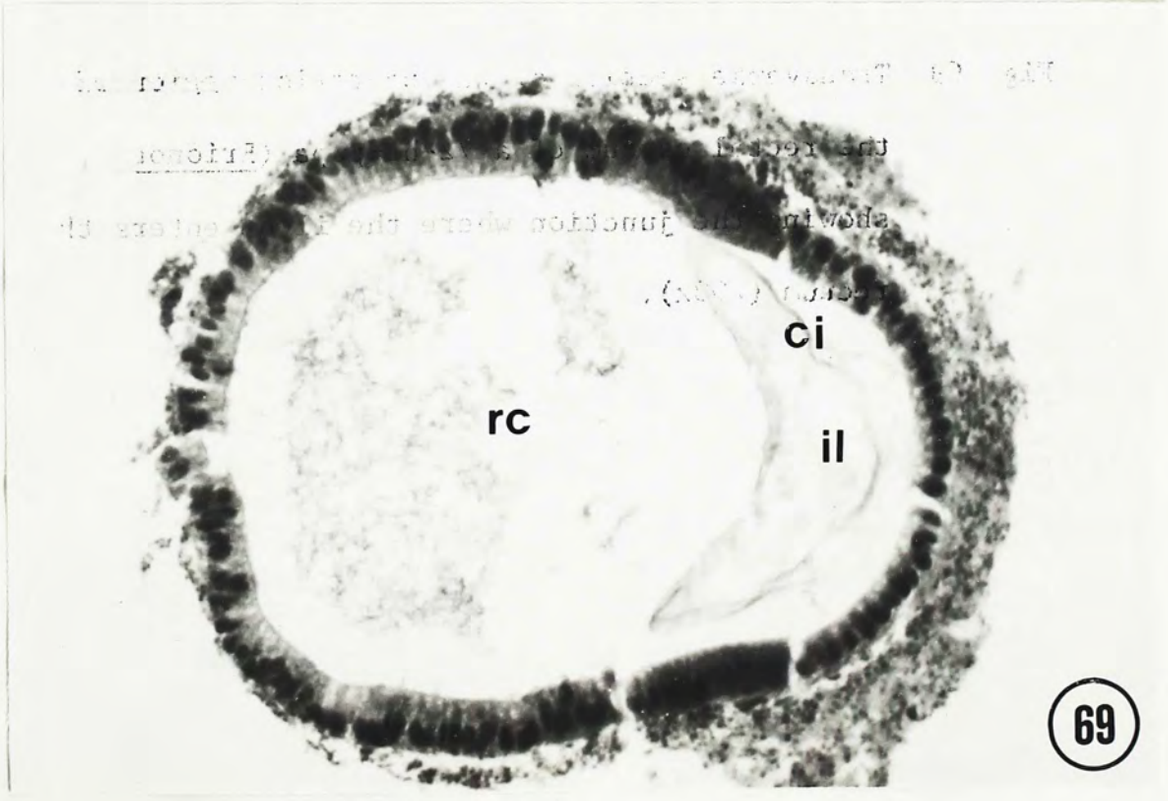
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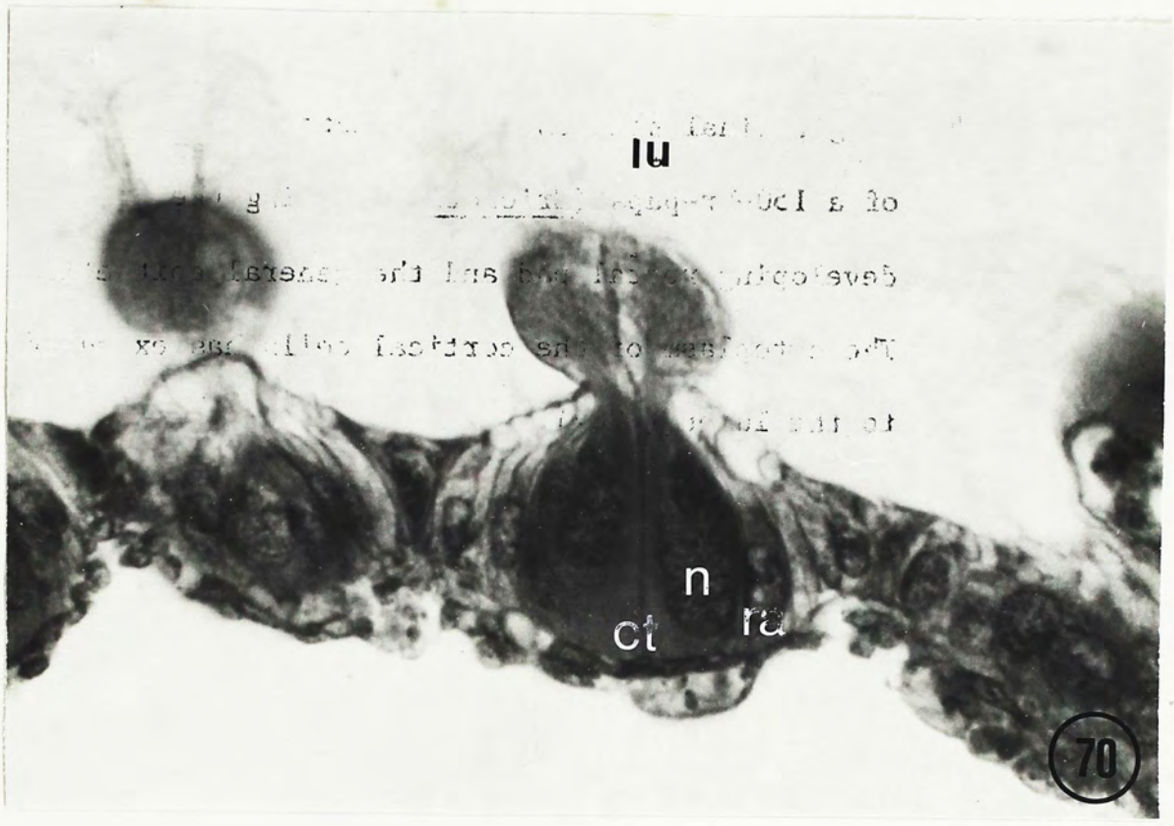
Fig. 70 Longitudinal section of the rectal epithelium of a 150-hr-pupa (Erionota), showing the developing rectal pad and the general epithelium. The cytoplasm of the cortical cells has extruded to the lumen (800x).

Fig. 71 Same as above. Note the developing rectal pad is composed of three cortical cells (800x).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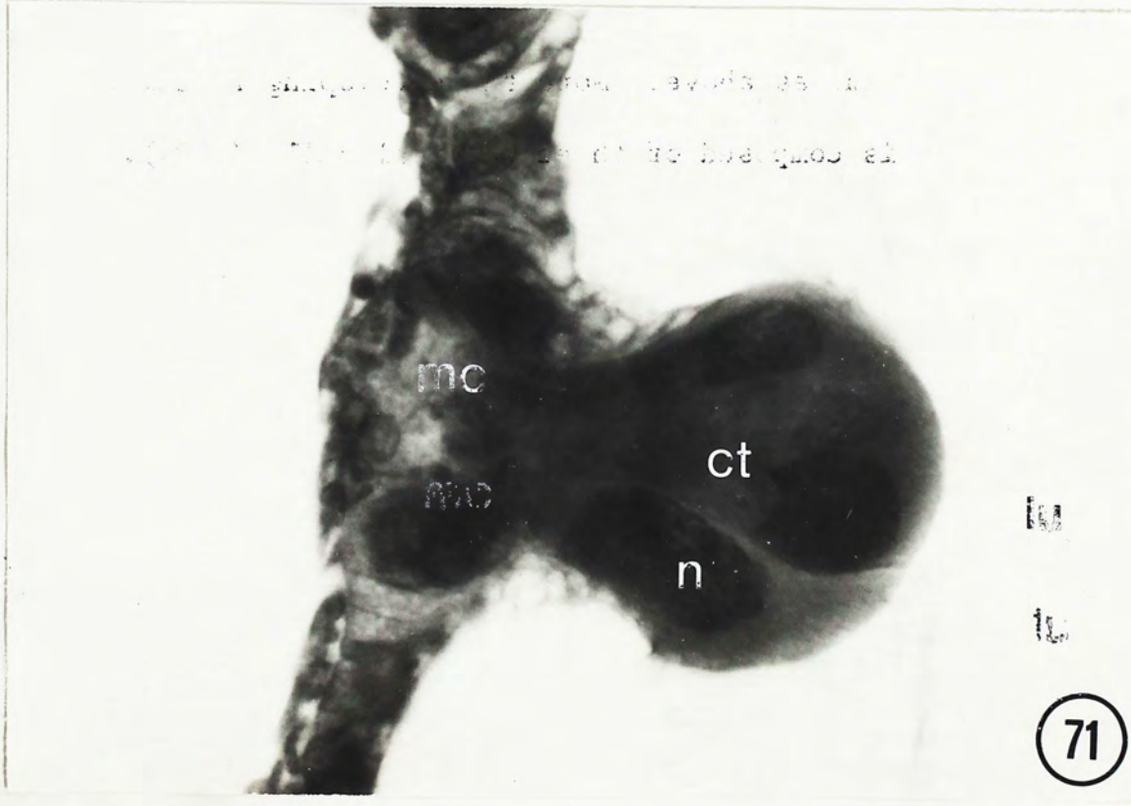
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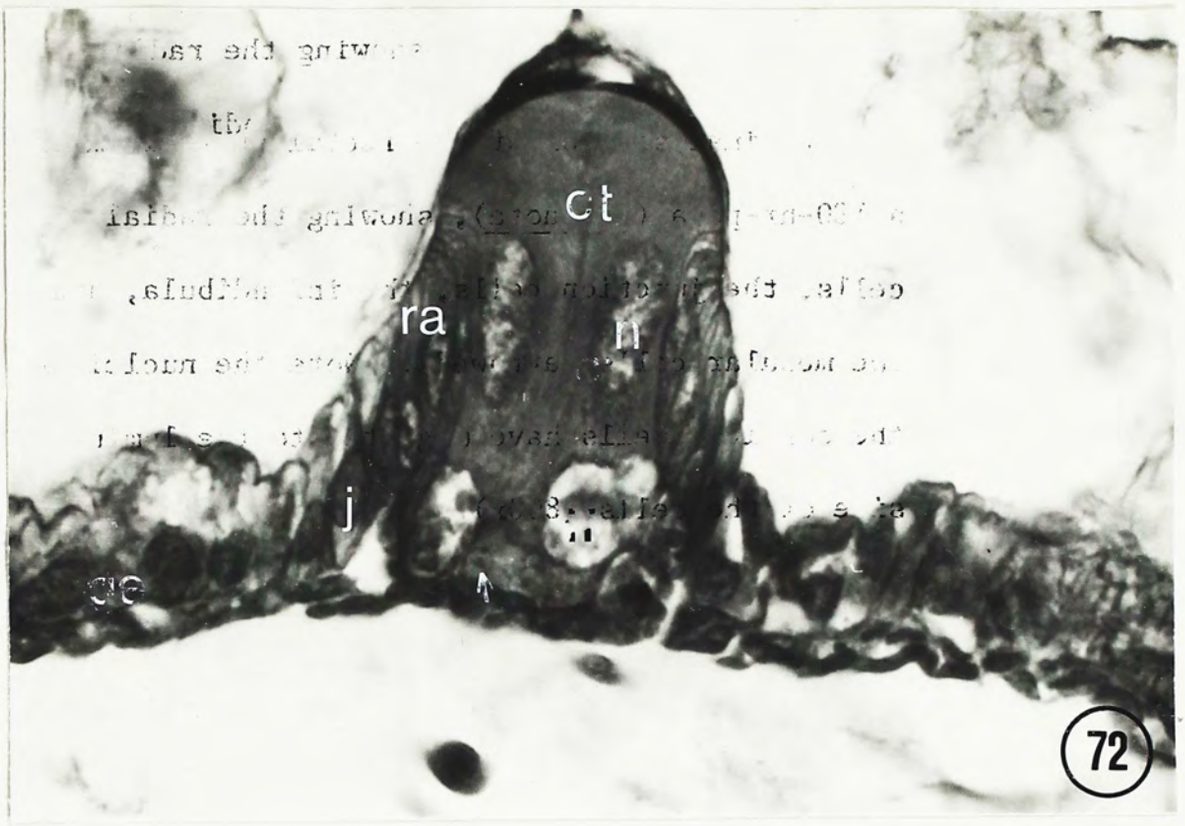
Fig. 72 Longitudinal section of the rectal epithelium of a 180-hr-pupa (Erionota), showing the radial cells, the junction cells, the infundibula, and the medular cells (arrowed). Note the nuclei of the cortical cells have migrated to the luminal side of the cells (800x).

Fig. 73 Longitudinal section of the rectal epithelium of a 220-hr-pupa (Erionota), showing the flattening of the cortical cells. Note the light-staining area (arrowed) between the nucleus and radial cells (800x).



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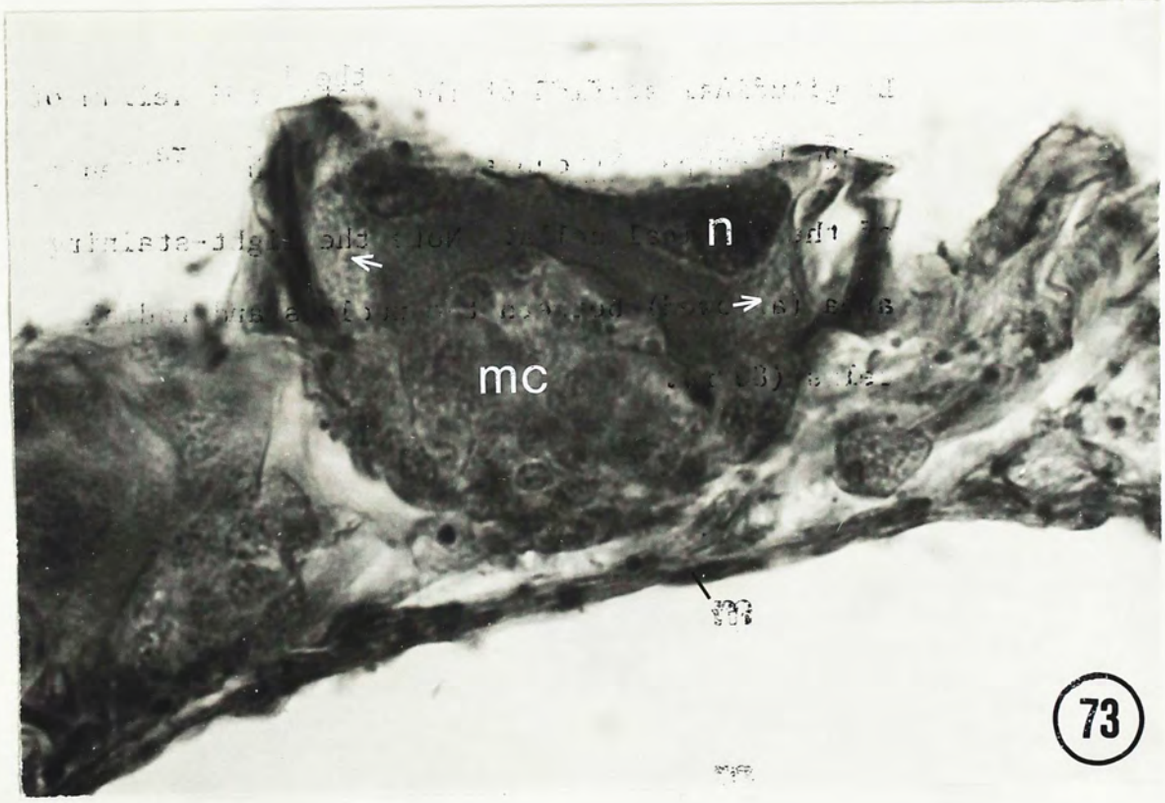

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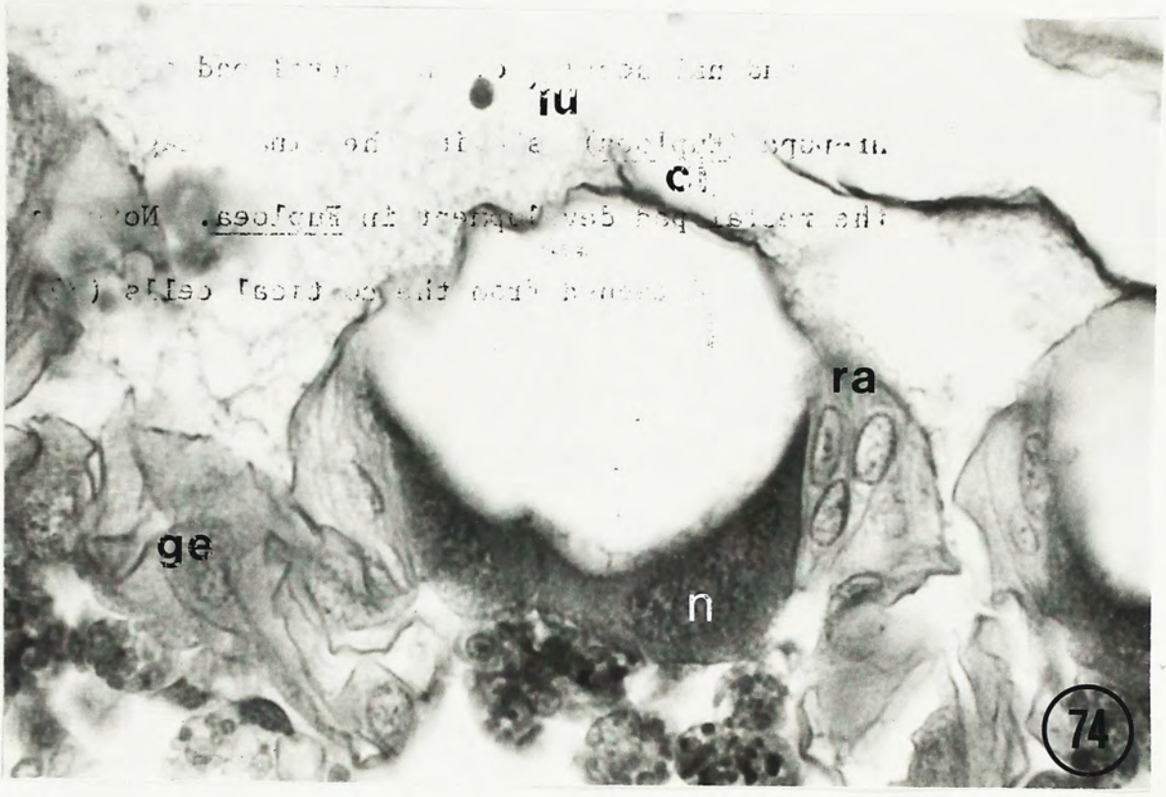
Fig. 74 Longitudinal section of the rectal pad of a 240-hr-pupa (Euploea), showing the final stage of the rectal pad development in Euploea. Note the intima is detached from the cortical cells (800x).

Fig. 75 Longitudinal section of the rectal pad of an adult (Euploea). Note variance of the structure of the rectal pad (800x).



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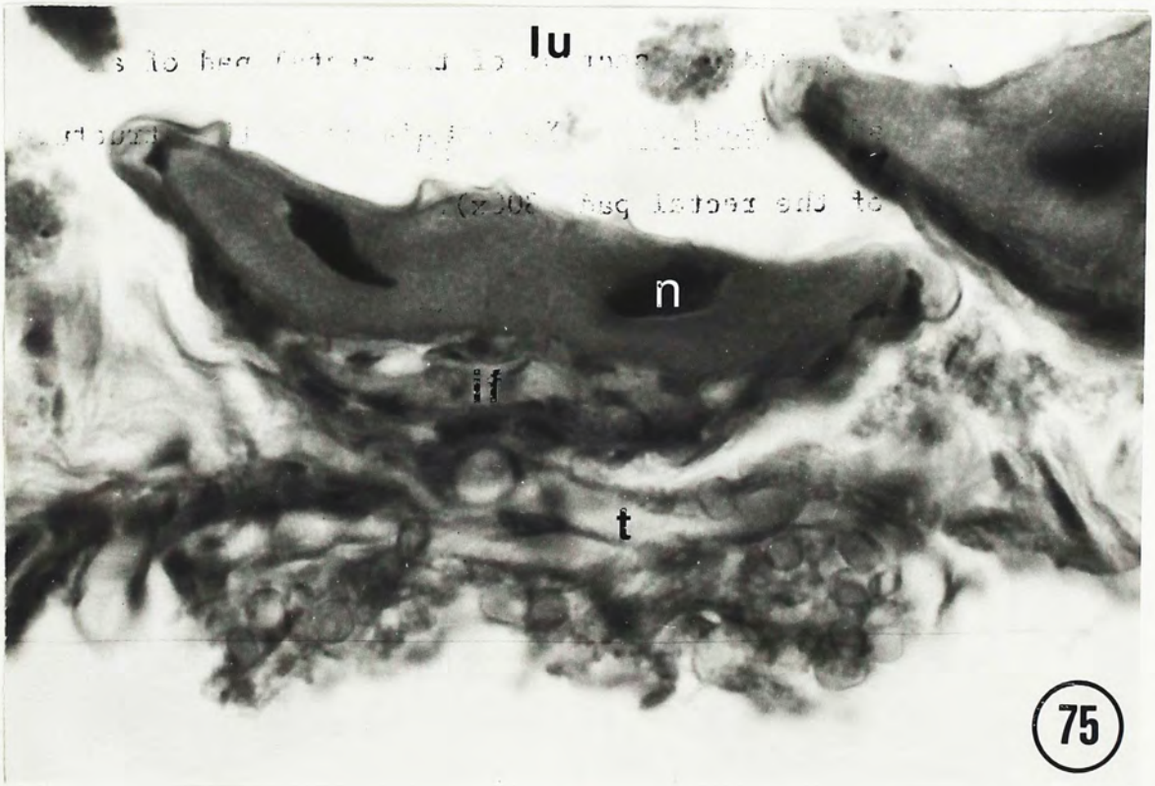

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PART III

GENERAL CONCLUSION

AND

SUMMARY

1. The larval guts of both Erionota and Euploea are typical of Lepidopterous larva in general and are believed to be a primitive form among insects.

2. As generally accepted, the foregut and hindgut are ectodermal in origin while the midgut is endodermal originated. All these regions join together to form a simple straight tube. These regions, however, perform their specific functions in the digestion of food materials.

3. The foregut of the larva serves merely as a tube that leads the food particles posteriorly and stores them temporarily before voided to the midgut. Unlike some other insects such as Blatta orientalis (Snodgrass, 1935), no cuticular teeth are present in the foregut. Thus, no physical digestion occurs here. Also, no digestive enzymes are secreted by the foregut epithelium.

4. The narrow foregut of the adult serves a continuous capillary of the siphon and provides assistance in the uptake of fluids by means of capillarity.

5. The midgut of the larva is undoubtedly the digestive and absorptive region of the gut. Nucleated and non-nucleated vesicles are found in the space between the epithelial wall

and the peritrophic membrane. Non-nucleated vesicles appear in dominance in the feeding larva while nucleated vesicles are more abundant when the larva becomes mature.

6. The hindgut of the larva is the region for faecal pellet formation and, at the same time, functions in reabsorption of water. Faecal pellets are formed in the ileum and the reabsorption of water takes place in the rectum effected by the cryptonephridial system.

7. Despite the degeneration of the cells of Region 4 and 5 of the oesophageal invagination, only condensation and rearrangement of cells take place in the foregut during the progress of metamorphosis. The hindgut also undergoes no degeneration of cells during metamorphosis.

8. The tall cells of the larval epithelium of the midgut are completely replaced by the regenerative cells. As a result of further development of the regerative cells during the prepupal stage, the epithelium of the larval midgut is sloughed to the lumen known as the yellow body.

9. The larval oesophageal invagination is unlikely served as valves in preventing regurgitation. However, three adult

structures are derived from the anterior imaginal ring during metamorphosis, they are: the adult crop, the proventriculus, and the adult oesophageal invagination.

10. Instead of forming the dorsal diverticulum as in Aedes (Romoser and Venard, 1967), Region 4 and 5 degenerate during the formation of the adult crop which is derived from the second region of the anterior imaginal ring.

11. The proventriculus of the adult is formed of the cells of region 2 of the anterior imaginal ring left after the formation of the adult crop.

12. The adult oesophageal invagination is formed by the folding of the double-layered posterior region of the developing proventriculus into the midgut shortly before adult emergence.

13. The adult crop probably serves to provide a compensatory mechanism for maintaining haemocoel volume during the expansion of the wings. Moreover, the crop may, at the same time, provides an assistance for aerostatic purposes.

14. The muscular adult proventriculus may function like the epiglottis of mammals to prevent the entry of air to the midgut.

15. The function of the adult oesophageal invagination is obscure. In Lepidopterous larvae, this structure is said to serve to ensure the food entering the peritrophic membrane. However, in the nectar feeding adults, the need for such a function is unknown. The only possible function for this structure is to provide assistance for preventing the entry of air to the midgut.

16. The midgut undergoes little change in the pupal stage. In the pupal stage, even when the insect is cut off completely from supplies of food, the midgut is still functional. The yellow body is stored in the midgut and is broken down gradually. Presumably, materials of the yellow body are reabsorbed and reused. Remnants are discharged to the hindgut in the pre-emergence stage.

17. The peritrophic membrane is not universally found in Lepidopterous adults. In the present study, the membrane is only present in adult Euploea with no known function. The membrane is produced by a ring of cells at the anterior end of the midgut. It is obvious that these cells continue to produce new membrane during the adult life after emergence.

18. The posterior imaginal ring, unlike the anterior imaginal ring, forms no adult organs for the insect.

19. After active mitotic activity, the larval ileum forms the slender, narrow pupal hindgut. The ileum is then mainly concerned with the reabsorption of water.

20. The rectal caecum and the rectal pouch are derived directly from the larval rectum. The epithelium of the rectal caecum is highly folded and is very flexible; this implies that the function of the rectal caecum is mainly for storage of metabolic wastes. It is generally believed that the rectal pads of the rectal pouch are responsible for the reabsorption of water in both the pupa and the adult (Wigglesworth, 1932, 1972; Judy and Gilbert, 1969, 1970).

21. The muscles that surround the alimentary canal of the larva undergo alterations during metamorphosis. The muscles of the foregut and the hindgut begin to degenerate shortly after pupation. Fragments of the muscles are phagocytosed by the pupal haemocytes, which are multinucleated masses, to form the spherules. However, no degeneration of the muscles of the midgut takes place during metamorphosis. The degeneration and regeneration of the muscles of the larval foregut and hindgut can be viewed as an adaptation to the mode of feeding of the insect. In the larva, the foregut is designed for the ingestion of rigid food clippings; the

hindgut is designed for the formation of faecal pellets and the reabsorption of water. These activities require strong muscle action. In the adult, the foregut is only a passway or a capillary for fluids; the hindgut is no longer needed for the formation of rigid faecal pellets. The strong muscle contraction is therefore no more a necessity.

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